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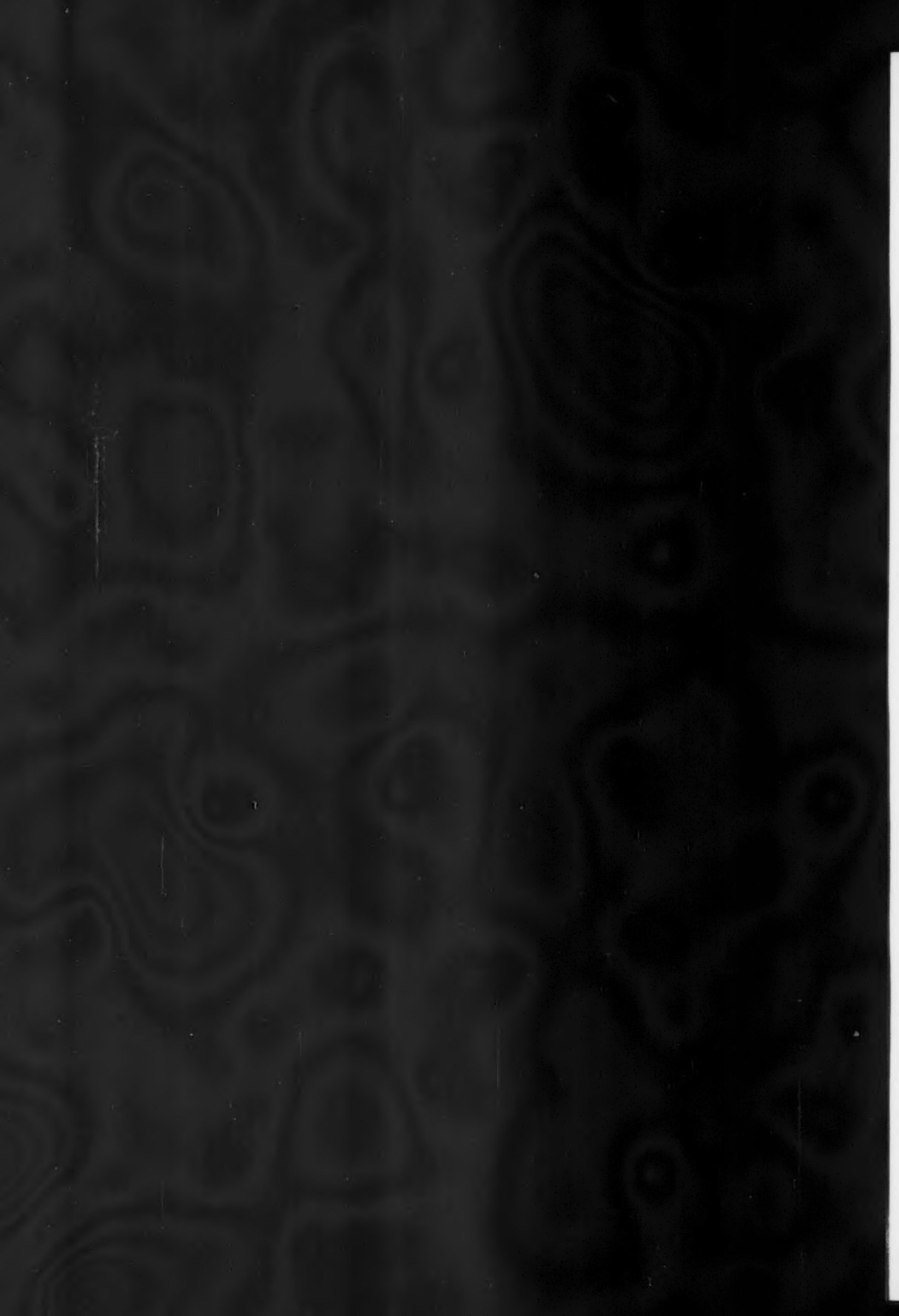
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PROOF OF THE EXISTENCE OF PRE-OVIPOSITAL EMBRYONIC DEATHS IN CHICKENS AND THEIR BEARING ON THE RELATION BETWEEN 'FERTILITY' AND HATCHABILITY¹

BY S. S. MUNRO² AND IGOR L. KOSIN³

Abstract

Although the terms 'fertility' and 'hatchability' refer in chickens to two biologically independent processes, in practice they are frequently found to be related. This type of association suggests that the two variables are related only through the mediation of a special set of conditions. The latter find their expressions in a low level of fertility and hatchability. It is suggested that under these conditions, a large proportion of 'infertiles' among hatching eggs are cases of pre-oviposital embryonic death. Evidence to support this has been provided by cytological study of the germ discs of such eggs. The germ discs were found to contain colonies of cells, indicating arrested but nonetheless genuine embryonic development. It has been shown, furthermore, that eggs of some hens are unfertilizable. On the basis of the present data it was possible to establish the existence of another peak in the embryonic mortality curve, occurring during the first $25 \pm$ hr. of zygotic development.

Introduction

Beginning with the pioneering work of Dryden (3), applied aspects of the phenomenon of fertilization in the domestic chicken (*Gallus gallus*) have received much attention from investigators. In practice, the term 'fertility' refers to the number of eggs that, following at least 24 hr. of incubation, on candling show presence of a developing blastoderm or 'germ spot'; 'hatchability' generally is used to denote the number of chicks hatched from the total eggs set. This usage allows for no distinction between the degree of 'fertility' and the hatching power of the fertilized eggs although the two, of course, are independent phenomena and from the practical standpoint each affects, in a specific way, the number of chicks that hatch from a given lot of eggs.

In recent years, particularly since the invention of the mammoth incubator and the advent of the commercial hatchery, 'fertility' has come to be regarded merely as a part of the broader 'hatchability' complex. This has led to a shifting of emphasis from the biological aspect of fertility *per se* and has also obscured the relative importance of its individual effect on the practical problem. From the biological standpoint, the terms fertility and infertility

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can be used only in absolute sense. To avoid confusion between the biological and practical definitions, it is proposed to refer to (biologically) fertile eggs as fertilized eggs. The practical definition of 'fertility' has already been given.

Among investigators, hatchability is generally used to denote viability of 'fertile' eggs during incubation and, by and large, has been regarded as quite independent of fertility. However, as we hope to show in this paper, the acceptance of candling as the method determining fertility, because of its essential crudeness, has led to considerable confusion in terminology and in the interpretation of data.

The term hatchability when used hereafter refers to the ability of 'fertile' eggs (as determined by candling) to hatch.

RELATION OF 'FERTILITY' TO HATCHABILITY

While, as previously stated and as pointed out by Pearl and Surface (17, pp. 105-164), fertility and hatchability are biologically independent, certain workers (Pearl and Surface (17, pp. 105-164), Knox (8), Munro (13)) have found them to be positively related. On the other hand, others (Hays and Sanborn (5, pp. 20-42), Jull (7), Hyre and Hall (6)) have found no relation. In our opinion this lack of agreement is explained by the fact that, at times, fertility (as judged by candling) and hatchability are positively correlated—often markedly so—while at other times there is no relation. This inconstancy of association, a phenomenon not uncommon in biological material, is due to the fact that the two variables, taking for granted the momentary and obvious dependency of the act of hatching upon the act of fertilization, are related only through the mediation of a special set of conditions that does not always exist.

TABLE I

RELATION BETWEEN FERTILITY AND HATCHABILITY IN BARRED PLYMOUTH ROCKS AND SINGLE COMB WHITE LEGHORNS

Barred Plymouth Rocks				Year	Single Comb White Leghorns			
No. of pens	Average		Co-efficient correlation		No. of pens	Average		Co-efficient correlation
	Fertility, %	Fertile eggs hatched, %				Fertility, %	Fertile eggs hatched, %	
11	83.0	78.7	+ .202	1939	12	83.6	79.0	+ .636*
14	84.6	56.8	+ .067	1940	12	80.1	43.0	+ .014
11	78.1	63.3	+ .382	1941	14	81.9	66.9	+ .400
19	84.6	76.8	+ .519*	1942	14	85.7	78.8	+ .238
13	82.6	79.0	+ .271	1943	12	82.6	83.8	- .105
16	80.4	68.2	+ .515*	1944	14	83.8	77.5	+ .443
Net correlation ($n = 72$)			+ .332**	1939-1944	Net correlation ($n = 66$)			+ .265*

* Indicates 5% level of significance.

** Indicates 1% level of significance.

There are considerable data at this institution showing a positive correlation between 'fertility' and hatchability. Table I summarizes the data showing this relation for the past six years in both White Leghorns and Barred Plymouth Rocks. The correlations are those existing between the means of individually mated pens. The males heading these pens are subject to a preliminary test and those that are found to give little or no 'fertility' are replaced. As can be seen, most of the correlations are low and, individually, only three reach the point of statistical significance. However, there is considerable variation, and the net correlations are significant.

In our experience, the relation is more pronounced between the means of mass mated pens when time was kept constant (Fig. 1), or between the means

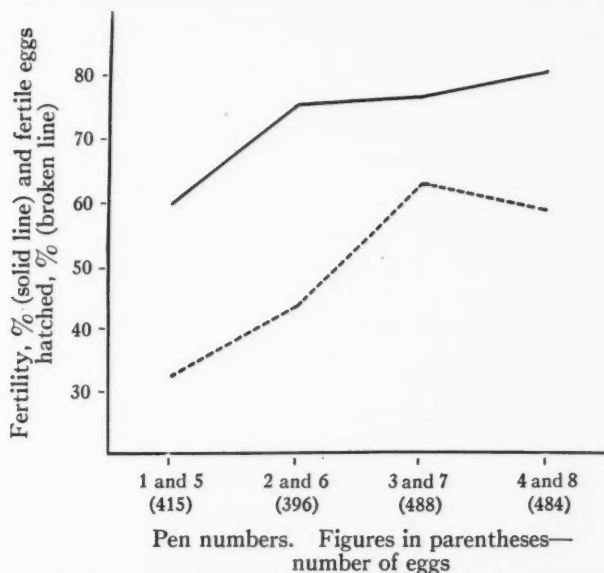


FIG. 1. Relation between fertility and hatchability in eight White Leghorn pens compared according to four treatment groups. This graph is based on the results of a single hatch.

of different settings from the same pen or groups of pens at different times (Fig. 2). High correlations between 'fertility' and hatchability also have been noted at times between the means of groups of eggs from the same pens that have been separated into shell strength classes by the specific gravity method (14). An example of this type of association is shown in Figs. 3 and 4. In fact, this tendency for 'fertility' to be correlated with shell strength provided some of the earliest evidence for the notion that at times a considerable proportion of embryos die while the egg is still in the oviduct of the hen, i.e. between fertilization and oviposition. Romanoff (18) makes a brief reference to this condition.

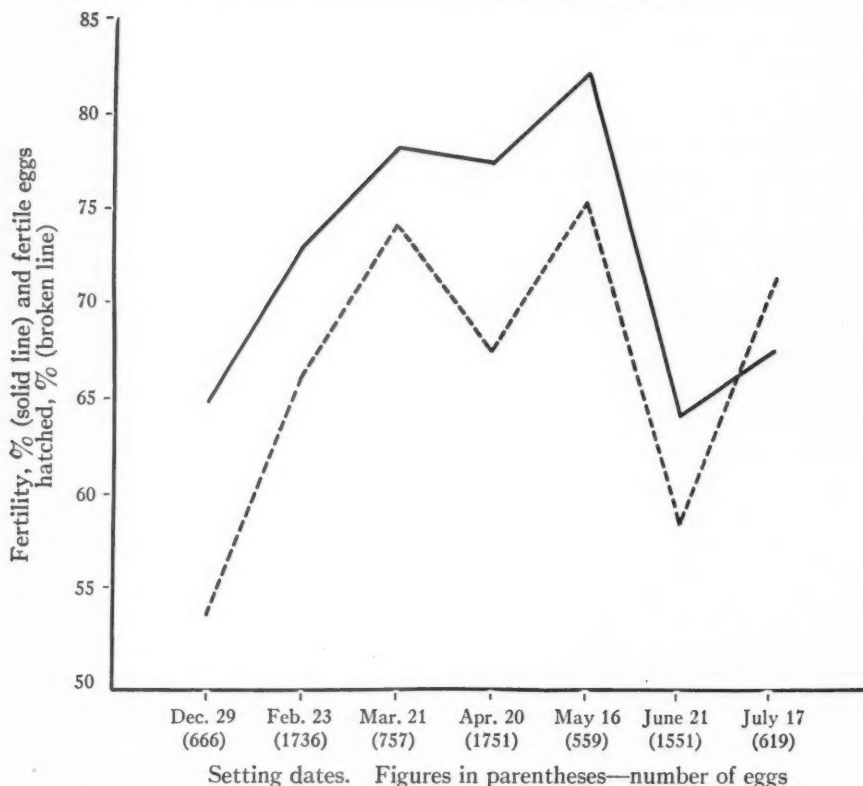


FIG. 2. Relation between fertility and hatchability in a mass mated White Leghorn flock. The data are based on the results of eight monthly hatches.

THE CONCEPT OF PRE-OVIPOSITAL BLASTODERMAL MORTALITY

Most investigators on the subject of fertility have identified 'fertility' by careful candling and (in some cases) have checked their results by breaking the eggs open and examining the germinal disc under a dissecting microscope. However, this procedure cannot distinguish embryonic deaths, which may occur between fertilization and oviposition, from the state of true (biological) infertility. Its accuracy, therefore, depends on whether or not and to what extent pre-oviposital deaths occur. That there is ample opportunity for the occurrence of such deaths is evident from the fact that between the act of fertilization and oviposition, the zygote spends approximately four or five hours in the magnum and isthmus of the oviduct, and another 20 in the shell gland. During this time thousands of cell divisions occur, and the originally unicellular zygote develops into a blastoderm that can be recognized as such by macroscopic examination (9) and (11).

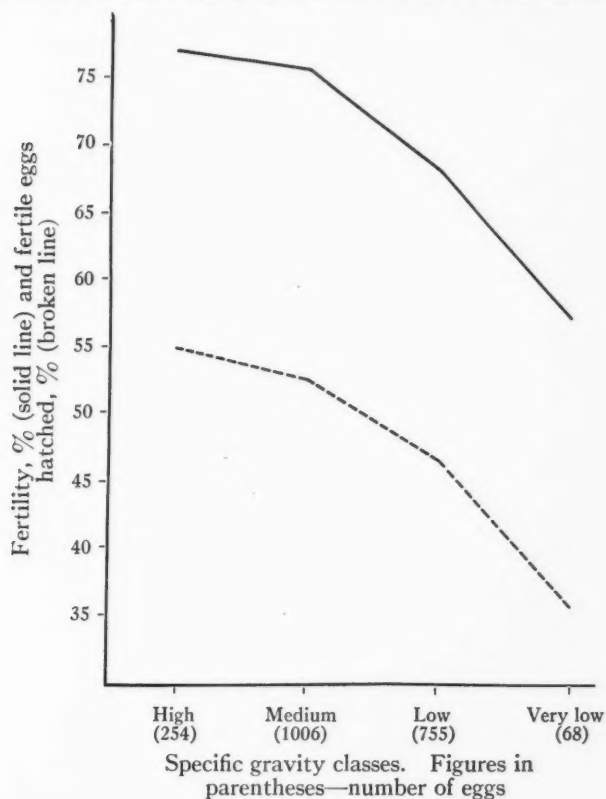


Fig. 3.

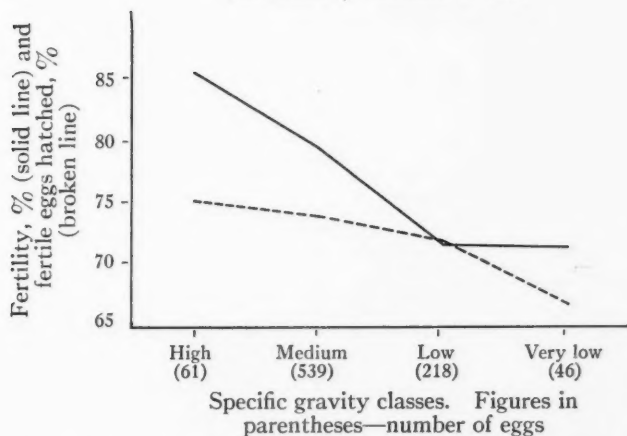


Fig. 4.

FIGS. 3 and 4. Relation between fertility and hatchability in a mass mated flock of White Leghorns. Eggs have been separated into four lots according to their specific gravity. Fig. 3—eggs set November 24, 1943; Fig. 4—eggs set January 26, 1944.

Material that is presented below offers cytological proof for the existence of such pre-oviposital blastodermal deaths.

Material and Methods

A series of low-'fertility'-low-hatchability hatches in a number of White Leghorn pens at this institution in 1943 provided favourable material for cytological studies.

The eggs from these pens were first separated (macroscopically) into 'fertiles' and 'infertiles' according to the recently described method (9). Yolks containing apparently infertile blastodiscs were then fixed in a 4% solution of formaldehyde for at least 48 hr. As a further check on the accuracy of classification, each blastodisc was stained *in toto* (for procedure see (9)). A few errors in classification were thus discovered and discarded. The remaining blastodiscs were lifted off the yolk (under water to prevent distortion) and transferred to 70% ethyl alcohol.

The usual routine of dehydration, embedding, and serial sectioning (at 7μ) then followed. Most of the blastodiscs were cut frontally; in this way all sections from one blastodisc can be accommodated on a 25×75 mm. slide. The staining procedure employed either Harris' or Delafield's haematoxylin and eosin. In all, more than 150 blastodiscs were sectioned and studied cytologically.

CYTOLOGICAL DETAIL

Unmistakable evidence of cellular proliferation, distinctly different from that found in the parthenogenetically developing avian blastodisc (10), was observed in approximately 50% of these so-called 'infertile' blastodiscs. In some cases, the proportion was as high as 75%.

The blastoderms were found to contain colonies or nests of cells that formed either compact nucleated yolk spherules, sharply demarcated from the surrounding medium (Fig. 5), or the more loosely bound cellular aggregates (Figs. 6, 7, 8). The size of the colonies varied, being never large, however. In many cases a single large colony was found to be accompanied by several smaller nests of cells. By comparison, the nuclear distribution in a normal blastoderm is more uniform as well as more extensive (Fig. 9).

The pattern of distribution of cells in larger colonies approached that of the normal blastoderm. It was more or less constant, in that the colonies limited themselves to the upper 15 to 20μ of the embryonic area. Within the area pellucida of the blastoderm, however, there were no specific loci for this

EXPLANATION OF FIGURES

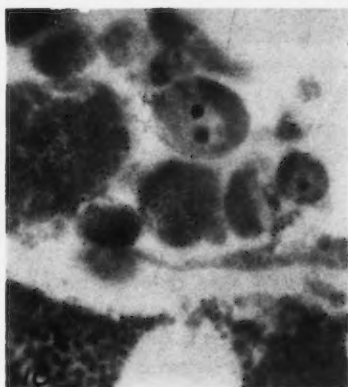
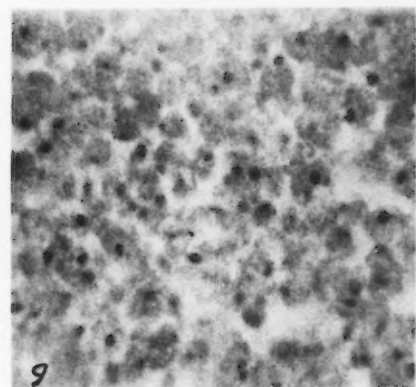
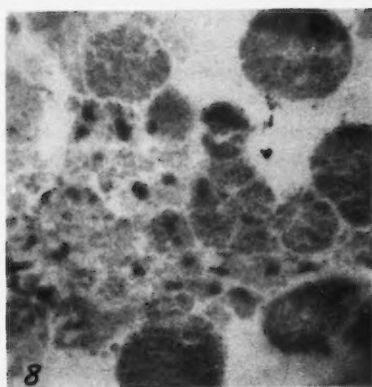
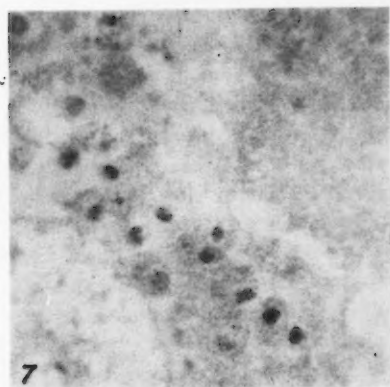
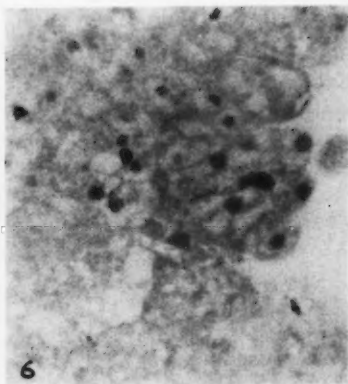
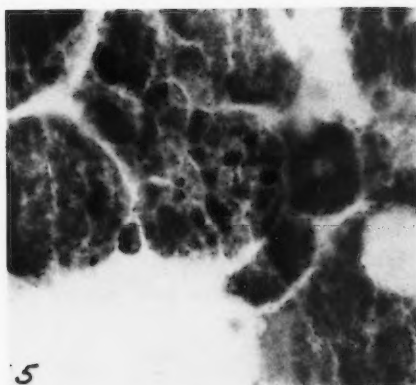
FIG. 5. A sharply demarcated colony of cells in the blastoderm of an 'infertile' egg. $\times 200$.

FIGS. 6, 7, 8. Examples of loosely organized cell colonies in blastoderms of 'infertile' eggs. $\times 200$.

FIG. 9. Cellular distribution in a normal non-incubated blastoderm. $\times 200$.

FIG. 10. A binucleate spherule in the blastoderm of an 'infertile' egg. $\times 200$.

PLATE I





occurrence. The impression was gained that the nuclei in the larger aggregates were more distinctly basophilic than those found in the smaller cell nests. Cytologically, the former also were more nearly normal. Pycnotic nuclei were infrequent. No significance was attached to the occasional presence of binucleate spherules (Fig. 10) as these are frequently found in apparently normal blastoderms. Some colonies (Fig. 7) contained nuclei that were about double the normal diameter. When present, this condition seemed to affect most of the nuclei in a colony. Because permeability of cellular membranes is known to increase at death, the appearance of 'bloated' nuclei was interpreted as a sign of approaching death of the colony.

No mitoses were seen in any of the specimens.

EVIDENCE FROM INDIVIDUALLY IDENTIFIED EGGS

During the 1944 breeding season there were, as usual, a number of hens in our regular pedigreed pens that gave either zero or a low degree of 'fertility.' These provided material for the following investigation.

The first step in investigating the cause of this phenomenon was to inseminate these hens artificially in order to determine the extent to which the absence of mating might be responsible for the condition. Accordingly, all males were removed from the pens and, after an interval of several days, individual samples of semen were collected from each male and inseminated into their respective pen mates. Following this treatment, many 'sterile' hens, as was anticipated, commenced to lay fertilized eggs, thus indicating the existence of preferential mating in the breeding pens. A few hens, however, remained 'sterile.' Next, the insemination was repeated to provide the necessary material for cytological study. This time only part of the hens in each pen were used, and these were made up of two sorts, first, low and zero 'fertility' hens (experimental birds) and, second, hens with normal 'fertility' (control birds). Moreover, the semen used in the test was a pooled specimen from all of the males, as a precaution against possible gametic incompatibility contributing to infertility. Results of the test are summarized in Table II.

It is apparent from the table that following artificial insemination, the level of 'fertility' was raised in the experimental group to approach that of the control lot. Some hens, however, continued to lay apparently infertile eggs some of which, when examined cytologically, were found to contain signs of blastodermal development. Three hens of the latter group, AA16, AA580, and A20909, were studied more intensively in that they were subjected to repeated inseminations of semen provided by different sires. Out of 21 eggs picked at random from a large sample, all 'infertile' by the macroscopic test, and laid by these hens over a period of almost three months, upon cytological examination, evidence of arrested development (pre-oviposital death) was found in nine germ discs.

TABLE II
NATURAL VS. ARTIFICIAL INSEMINATION IN 'POOR' BREEDERS

Pen	Experimental					Control		
	Natural mating			Artificial insemination		Insemination		
	No. hens	Fertile	Infertile	Fertile	Infertile	No. hens	Fertile	Infertile
A*	2	2	26	0	2 (2)**	0	0	0
C	1	6	7	5	1	3	13	0
E	1	1	4	1	0	2	12	0
G	2	2	24	0	10 (5)	2	8	4
I	3	17	20	13	0	1	3	3
K	1	7	17	4	1	2	11	0
M	1	8	14	6	0	3	8	2 (1)
O	1	10	10	4	1	2	5	9 (2)
U	2	7	14	5	1	2	7	1
Total		60	136	38	16 (7)		67	19 (3)
		(30.6% F.)		(70.4% F.)			(77.9% F.)	
B	2	3	12	3	3 (2)	2	7	7 (2)
H	2	31	15	10	0	1	3	3 (2)
J	2	9	13	3	0	3	14	2 (1)
L	2	8	23	1	7 (2)	2	6	3 (3)
N	2	11	11	8	4 (3)	1	6	1
P	3	10	29	6	9 (6)	2	10	4 (4)
R	1	14	12	4	2 (2)	2	7	0
V	2	4	3	4	3 (1)	1	2	0
EX 1	1	0	23	4	3 (1)	2	9	0
Total		90	141	43	31 (17)		64	20 (12)
		(39.0% F.)		(60.9% F.)			(76.2% F.)	

* Pens A, C, E, G, I, K, M, O, U—White Leghorns.

Pens B, H, J, L, N, P, R, V, EX 1—Barred Plymouth Rocks.

** Numbers in parentheses—fertile, on cytological examination.

Discussion

The existence of oviducal mortality, long suspected on the basis of theoretical considerations and now proved to be a fact, following cytological study of 'infertile' hatching eggs, suggests re-examination of some of the present day views regarding fertility in the domestic chicken. The new knowledge stresses the importance of maternal influence on the ontogeny of the zygote, in so far as it is instrumental in providing it with an adequate micro-environment. It is questionable whether heredity, in the accepted sense of the word, plays an important role in the occurrence of pre-oviposital mortality. Our experience shows that it is characterized by extreme inconstancy of appearance in a given population. While one might be tempted to speculate about the influence of gene-environment interactions upon phenotypic expressions, this would only lead into rather obscure recesses of physiological

genetics and morphogenesis, two almost completely unexplored fields of knowledge in so far as the domestic chicken is concerned. Furthermore nothing definite is known about the possible agents which, *in vivo*, apparently can so profoundly alter the developmental pattern of a successfully fertilized ovum. One fact, however, seems to be clear and this is that conditions that are conducive to high hatchability also favour high fertility, the situation indicative of low proportion of oviducal deaths in flock mated pens.

If an appreciable proportion of embryos die pre-ovipositally and if the death rate varies at different times, we have a plausible explanation for the observed correlation between specific gravity, hatchability, and 'fertility' (14, 15). Apparently whatever is responsible for the inability of the egg to support the developing embryo is, at least partly, reflected in shell strength. This is logically explained by assuming that the normal egg that gives rise to a chick is formed and ovulated at a time when the hen is physiologically normal. Such an egg has a strong sound shell. The physiologically subnormal hen, however, produces 'poor' quality eggs that cannot support the developing embryo. It seems probable that the chemical make-up of such eggs is deficient and the shells are also 'subnormal.' Thus, shell quality is a mirror of internal egg quality because both depend on the physiological state of the hen. Seasonal variations in the fertility-hatchability relation support this concept. If the process of fertilization were independent of the physiological status of the hen at any specific time, there is no *a priori* reason why it should be related to shell strength.

In a recent paper one of the authors (16) reported 'fertility' and hatchability data from a series of single mated White Wyandotte pens that showed a very marked association between 'fertility' and hatchability. In this particular case the evidence indicated that the low 'fertility' and hatchability, which characterized half the females in each pen, could not be ascribed to the male, but, rather, was caused by the previous (rearing) history of the females. It was suggested that "many of the eggs were either (a) unfertilizable or (b) incapable of supporting the zygote to the stage where fertility can be detected."

The condition of 'unfertilizability,' suggested by Sampson and Warren (19), could be brought about in two ways: (a) the egg itself could be incapable of being activated by the sperm, either because it is already moribund or dead, or through the lack of some vital constituent in its immediate environment, such as enzyme (the possible importance of hyaluronidase in fertilization is suggestive (4 and 12) or (b) because the spermatozoa are killed or rendered biologically inactive before they reach the site of fertilization.

Underlying all this discussion is a fact that there is no clear-cut division between the pre-oviposital and the post-oviposital stages of development.

The fact that the term 'incubation' is limited to 21 days has been accepted purely for practical reasons; biologically, no such rigid division exists, because embryonic development commences from the moment the two gametes unite to form the fusion nucleus. The developmental process then goes on continually until it is either resolved by hatching, or is terminated prematurely.

It has been already shown that in some cases the proportion of pre-oviposital deaths has been found to rise to 75% of the 'infertile' eggs examined. This makes it possible to establish the existence of another peak in the embryonic mortality curve, one occurring during the first $25 \pm$ hr. of zygotic development.

Developmental morphology of these deaths is not clear. The early, undifferentiated blastoderm can be likened to an actively proliferating colony of cells, which, as in the case of an *in vitro* tissue culture, requires certain optimum conditions in its milieu for maintenance and growth. If these conditions are lacking, then the normal process of growth never gets under way or, if in operation, soon ceases save, possibly, for isolated islets of surviving cells. Examples of the latter situation have been described by Das (2) and Byerly (1). It is possible, therefore, that the cell colony or cell nests of the 'dead blastoderm' are the expression of an analogous condition in the hen's ovum.

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A REVISION OF THE FAMILY ACARIDAE (TYROGLYPHIDAE), ORDER ACARI, BASED ON COMPARATIVE MORPHOLOGICAL STUDIES

PART I. HISTORICAL, MORPHOLOGICAL, AND GENERAL TAXONOMIC STUDIES¹

BY HERBERT H. J. NESBITT²

Abstract

The purpose of this paper is to lay the basis for some serious work on comparative acarology. For this purpose a restricted group, the family Acaridae, has been selected and a detailed morphological study based on approximately 40 species, representative of the various genera of the family, is presented. It is hoped that this will demonstrate more clearly than has hitherto been done the significance, from the standpoint of classification and phylogeny, of the principal morphological characters present in this group of animals. The classifications of previous workers, particularly that of Oudemans', are briefly reviewed and evaluated in the light of present findings; a discussion of the composition and inter-relationships of the various genera and higher groups is given; and finally a synopsis of the tribes and genera of the family Acaridae, based on characters believed to be of phylogenetic significance, is presented.

Introduction

Except for tentative beginnings by Trägårdh (45), comparative acarological studies have been eschewed by most zoologists. This is regrettable as many taxonomic blunders could have been avoided if a serious study had been made of the morphology and ecology of mites. This paper is the first of a series that I plan to devote to the systematics of the Acari, in an effort to demonstrate that, if sufficient attention is paid to the anatomy and biology of mites, a natural system of classification can be discovered that illustrates the relationship of the various groups.

The family *Acaridae* (*Tyroglyphidae*) of the suborder *Sarcoptiformes*, cohors *Diacrotricha*, was chosen as the subject of these initial studies for several reasons. First, the small number of species and the simplicity of the individuals aid considerably in an understanding of the structure of the primitive body, the establishment of homologies, and the tracing of relationships in the group. Secondly, the extent of the damage that these mites cause to grain and farinaceous products in storage labelled them as economic pests and warranted a thorough investigation of their habits and systematic position. For several years the taxonomy of this group has been in a hopeless

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The subsequent parts of this paper will deal with the genera mentioned in the synopsis (pp. 175-178). An effort will be made to give an adequate description of the various North American and European species but because of the difficulty of obtaining suitable specimens little attention will be paid to tropical and exotic forms. It is expected that Part II, which treats of the genus *Caloglyphus*, will appear in the near future.

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muddle because many of the original descriptions were so vague that few correct identifications could be made. Thirdly, it was an advantageous group to study because the Dutch investigator, Dr. A. C. Oudemans, had contributed greatly to the solution of many of the problems by his painstaking and thorough work. Whilst accepting many of Dr. Oudemans' groups and part of his system of classification, I am unable to agree with his general conclusions. It is my belief that the system of classification that he advanced is highly artificial and, therefore, unstable. To illustrate my arguments a careful morphological study has been made of about two score of species—all that were available. To save space and endless repetition, 12 of these were chosen for description and illustration as representative of the genera involved.

The members of the family Acaridae are notable for the extent of their distribution. They are found in all types of habitat from Arctic tundra to tropical rain forests and wherever man in his wanderings has taken mites in his food and produce. Living on all kinds of organic substances, these creatures are commonly found infesting such materials as preserved meats, cured and raw hides, organic powders, seeds, and farinaceous products. In stored grains they cause great economic loss not so much by what they eat (though populations of astronomical figures are found at times) as by the damage that they cause by changing the moisture content of the medium and initiating the growth of moulds. In the state of nature they are usually found on rotting leaves and plant debris, on the bark of trees, on decaying bulbs and tubers, on fresh and putrid mushrooms, and in the nests of mammals and birds, where presumably they live on organic wastes and bits of hair and feathers. In speaking of ecological niches it is interesting to note that, even as the family may be divided taxonomically into two quite distinct sub-families on morphological grounds, it may also be separated into the same two subfamilies on the basis of the type of habitat preferred. Almost without exception the members of the one group prefer to live in substances having a low moisture content (20 to 30%), viz., wheat, seeds, and stored farinaceous products, whereas the members of the other group can exist only in a very humid habitat, many seeming to prefer a place where they are wading in a film of water. As a result of these studies I am persuaded that the members of the former group can and do eat the more solid organic substances such as the germ and endosperm of seeds, whilst those of the latter group live fairly exclusively on the fungi and moulds growing on the excessively damp substratum that they prefer. Furthermore, many eat dead and decaying insects, the Caloglyphids being the most notable example. Apart from a few species of the genus *Thyreophagus*, which live on oyster-shell scale and kindred insects, none of the family appears to be either a predator or a parasite. Unlike either the *Eriophyidae* or *Tarsonemidae*, none of these mites has been found living on plant tissue*. As yet no fossil records have been found of either the Acaridae or their immediate progenitors, but this is not to be wondered

* A few have been reported on plants, but in view of the circumstances under which these were found and the notes pertaining to them, it would appear that they were accidental pests.

at, as they are extremely small creatures, which do not lend themselves to easy fossilization.

In organization the members of this family are very simple. They are minute, soft-bodied creatures that lack eyes, heart, respiratory organs, and complex sensory receptors. They range in size all the way from minute beings less than 0.1 mm. in length to the relatively huge female Caloglyphids that may attain a length of 2.0 mm.

Materials and Methods

The specimens for this study were collected from samples of wheat, seeds, and debris that were taken from ocean and lake boats by the inspectors at the various Canadian ports of entry. In addition, considerable collecting was done in green-houses, woods, bogs, gardens, and such likely spots. To supplement this collection specimens were borrowed from Dr. H. E. Ewing of the Bureau of Entomology and Plant Quarantine, Washington, D.C.; Mr. S. G. Jary, of the Southeastern Agricultural Experiment Station, Wye, England; Dr. Philip Garman of the Connecticut Agricultural Experiment Station, New Haven, Conn.; the late Mr. A. C. Davis of the United States Department of Agriculture, Beltsville, Maryland; and Dr. Clarence E. Mickel of the Department of Entomology of the University of Minnesota. A thorough examination was also made of the type material of the species described by Mr. N. Banks in his *Revision of the Tyroglyphidae of the United States*.

All mites intended for storage were killed and preserved in Oudemans' mounting medium*. Specimens for immediate study were mounted temporarily in a chloral hydrate fixing and clearing fluid.** For permanent preparations, they were transferred to Womersley's modification of Berlese's mounting medium***. After the gum arabic had dried sufficiently the cover slips were ringed with Murrayite.

All the drawings were made with an Eddinger apparatus supplemented with a camera lucida. To determine the nature of the setae, and in particular some of the smaller, more tenuous ones, which are relatively invisible in ordinary light, a polarizing microscope has been found to be most effective.

* Oudemans' mounting medium:

- 87 cc. 70% ethyl alcohol.
- 5 cc. glycerine.
- 8 cc. glacial acetic acid.

** Chloral hydrate clearing solution:

- 40 gm. chloral hydrate.
- 25 cc. water.
- 2.5 cc. hydrochloric acid.

*** Womersley's modification of Berlese's mounting medium:

- 100 cc. distilled water.
- 40 gm. gum arabic.
- 50 gm. chloral hydrate.
- 10 gm. glucose syrup.
- 30 gm. phenol (Womersley uses 50; I have found 30 slightly better).
- 20 cc. glacial lactic acid.

History

Prior to 1900 the principal systems of classification in use were those designed by Canestrini (6, 7, 8), Kramer (8, 18), and Berlese (4). In 1901-3 the most famous of the English works appeared, from the pen of Michael (23). The following year saw the publication of the first of Banks' (1) treatises, which was followed in 1906 (2) by his revision of the Tyroglyphidae. Since Oudemans has incorporated in his subsequent publications the best features of the systems that these workers devised, there is little need to discuss them separately, apart from commenting on the debt of gratitude that we owe to Michael, for his painstaking work on the Oribatidae and Tyroglyphidae, and to Banks for the practical usefulness of his keys. Should the reader desire a thorough and complete history of the subject he is referred to the first volume of Michael's *British Tyroglyphidae* or Oudemans' *Kritisch historisch overzicht der Acarologie* (Pt. I-III) (36, 38, 40).

In the following pages the more recent systems of classification by Oudemans, Sig Thor, Vitzthum, and Zakhvatkin will be examined and an effort will be made to give a fair and just estimate of each. Because Oudemans has been the greatest contributor in this field and because he has had the greatest influence, his work will be discussed at some length. Many of his groups will be discarded, some because they are outside the limits of the family Acaridae, as we now define it, others because they are based on spurious morphological characters, which neither warranted their erection nor justified their perpetuation. As a result of my work I am of the opinion that whilst we should be grateful to Oudemans for his excellent work there are many features in his system of classification that ought to be changed. Accordingly, I have criticized his keys and presented alternative schemes that I believe are justified.

Oudemans.—Since the turn of the century Oudemans has devoted a great portion of his time to the systematics of the acarid mites. In 1906 (24) he laid the basis for his modern system of classification by splitting the suborder Cryptostigmata Berlese 1896* into the two "supercohortes"—Acaridae Latr. 1806 and Oribatei Dug. 1834. The former of these was again subdivided into three "cohortes" the *Anacrotricha*, *Monacrotricha*, and *Diacrotricha*, on the basis of the number of vertical hairs. In 1908 (25) he brought out a new classification of the Acaridae** in an effort to clear up the confusion that had resulted from his attempt to fit *Syringobia* into Kramer's classification in *Das Tierreich*. Here again he separated the genera and subfamilies of the Acaridae (Sarcoptidae) on the basis of the number of vertical hairs but did not apply the terms *Anacrotricha*, etc., which he had adopted in his previous work. Keys were presented to divide the supercohort Acaridae into 18 families and these into their respective genera.***

* Subsequently *Sarcoptiformes* Reuter 1909.

** This was to supersede and include the keys of 1901 and 1903.

*** The Tyroglyphinae may be separated either by the hypopi or the adults.

Apart from slight additions to this system, and some species description, little further work of a general nature on the Tyroglyphidae was attempted until 1923 (29), when he proposed that a family be erected for the genus *Rhizoglyphus* Clap. 1869. The genus *Tyroglyphus* was left in the old family Tyroglyphidae.

Oudemans' first comprehensive work on the Diacrotricha came in 1924 (30), when he published his *Analytical key for the classification of families and genera of the Diacrotricha Oudms. 1906 (Acari)*. The parts of the key that concern this paper are included below.

Cohors Diacrotricha Oudms. 1906

- A. 1. Skin polished, or dull, or chagrined, or rough, or scaly, only in a few hypopi and nymphae partly finely striated, or wrinkled. Larvae usually with „Bruststiele“ or „Urstigmata.”
- B. 1. Body more or less *Tyroglyphus*-shaped; skin polished, seldom finely granulated; mandibles normal, chelate.
- C. 1. Ambulacra with caruncle and movable claw, both sessile. *Tyroglyphidae* Donn. 1868. [*]
- C. 2. Ambulacra with claw only.
- D. 1. Claw of legs I and II sessile, *Rhizoglyphidae* Oudms. 1923. [**]

Despite the naturalness and simplicity of the above key there are certain difficulties involving that group of mites that will eventually be included in the genus *Caloglyphus*. As the caruncle in these forms is intermediate in size between the rather full billowy structure found in the Tyroglyphidae and the meagre almost non-existent caruncle of the Rhizoglyphidae, their classification is difficult because different types of fixative and methods of orientation could artificially place these in one or the other of the above families.

Furthermore the key is too general and lacks the exactness that his subsequent systems of classification usually have. As a result of this, five of the 10 genera of the family *Rhizoglyphidae*, viz., *Ceroglyphus*, *Histiogaster*, *Stereoglyphus*, *Suidasia*, and *Valmontia*, were transferred to the family Tyroglyphidae in the next key (33), the better to explain their relationship. Also, since no mention is made of the male anal copulatory suckers, the genus *Saproglyphus* could be included.

Later in the same year (33), he published a much fuller key devised to include the new family Tyrophagidae Oudms. 1924, which was erected to include the mites of the genus *Tyrophagus* Oudms. 1924, i.e., certain mites of the “putrescentiae” grouping of the old genus *Tyroglyphus*. As this key and the later key of 1927 (37) have several features in common, they are placed together below for the sake of comparison.

* Included in this family are the genera: *Tyroglyphus* Latr. 1796, *Scatoglyphus* Berl. 1913, and *Monieziella* Berl. 1898.

** Included in this family are the genera: *Stereoglyphus* Berl. 1923, *Rhizoglyphus* Clap. 1869, *Schwiebea* Oudms. 1916, *Petzschia* Oudms. 1923, *Suidasia* Oudms. 1905, *Saproglyphus* Berl. 1890, *Valmontia* Oudms. 1923, *Acaridina* Van Ben. 1870, *Eberhardia* Oudms. 1924, *Histiogaster* Berl. 1883, and *Ceroglyphus* Vitz. 1919.

(Quoted from Entomol. Ber. 6 (139) : 301. 1924) (Ref. 33).

A. 1. Skin (except in a few nymphae, incl. hypopi) not finely wrinkled or striated (Murray 1877).

B. 1. Mandibles chelate.

C. 1. Ambulacra with (so called) sessile claw, with or (so called) without sessile caruncle; body more or less *Tyroglyphus*-shaped; with line of demarcation between propodo- and hysterosoma; with propodosomatic shield (if not visible use 1% caustic kali); ♀ genital aperture between coxae III and IV.

D. 1. The longer body-hairs are loose, whip-shaped.

E. 1. ♂ with suckers near anus and on tarsi IV. Larvae with „Bruststiele.”

F. 1. Nuchal hairs dorsal, on level of trochantères I, minute, smooth, or absent. Skin polished.

G. 1. Legs without or with spines; if present (pay attention to underside of tarsi!) they may be long, but are never robust; before the olfactory club on tarsi I and II no spine. *Tyroglyphidae* Donn. 1868[*].

G. 2. Legs short and thick, with robust spines; before the olfactory club on tarsi I and II such a spine. *Rhizoglyphidae* Oudms. 1923 [†].

F. 2. Nuchal hairs marginal on a level before trochantères I; skin polished or granulated; moreover as G. 1. above. *Tyrophagidae* nov. fam. [††]

E. 2. ♂ without suckers near anus, nor on tarsi IV; larvae without „Bruststiele” (?); skin polished. *Saproglyphidae* nov. fam.

* Oudemans includes the following genera in this family: *Stereoglyphus* Berl. 1923, *Histiogaster* Berl. 1883 (incl. *Monieziella* Berl. 1898), *Valmontia* Oudms. 1923, *Tyroglyphus* Latr. 1795, *Caloglyphus* Berl. 1923, *Olafsenia* Oudms. 1924, *Ceroglyphus* Vitz. 1919, *Suidasia* Oudms. 1925, & ? *Froriepa* Vitz. 1919.

** In a subsequent publication (39) Oudemans makes a correction: “These should read --- F. 1 and F. 2.” “Just before . . . etc.”

† This family includes the following genera: *Rhizoglyphus* Clap. 1869 and *Schwiebea* Oudms. 1916; *Garsaultia* Oudms. 1916, and *Sancassania* Oudms. 1916, both based on hypopi.

†† Oudemans includes the following genera in this family: *Tyrolichus* Oudms. 1924, *Tyroborus* Oudms. 1924, *Tyrophagus* Oudms. 1924, *Povelsenia* Oudms. 1924, and *Ebertia* Oudms. 1924.

(Quoted from Entomol. Ber. 7 (157) : 243. 1927) (Ref. 37).

A. 1. Skin (except in a few nymphae, incl. hypopi) not finely wrinkled. Murray 1877.

B. 1. Mandibles chelate.

C. 1. Ambulacra with so-called sessile claw and sessile caruncle; the latter may be very small; body more or less *Tyroglyphus*-shaped; with line of demarcation between propodo- and hysterosoma; with propodosomatic shield; ♀ genital aperture between coxae III and IV; ♂ genital aperture between coxae IV, with suckers near anus and on tarsi IV; Larvae with „Bruststiele.”

D. 1. The longer body-hairs are loose, whip-shaped; in young stages often stiff, rod-like!

E. 1. Cervical hairs dorsal, on a level with trochantères I, minute, smooth, or absent; skin polished.

F. 1. [**] Before the olfactory club on tarsi I and II no spine; legs with or without spines; if present, they may be long, but are never stout and conical. *Tyroglyphidae* Donn. 1868.

F. 2. [**] Before the olfactory club on tarsi I and II a stout conical spine; legs short and thick, with robust spines. *Rhizoglyphidae* Oudms. 1922.

E. 2. Cervical hairs marginal, on a level before trochantères I, minute, smooth; tarsi ventridistally with minute spines. Skin granulate. *Ebertiidae* Oudms. 1927.

E. 3. Cervical hairs marginal, on a level before trochantères I, long, hairy, directed forward and curved inward and downward; skin polished; tarsi ventrally (occasionally also dorsally) and distally with minute spines. *Tyrophagidae* Oudms. 1924.

As the 1927 key is simply a revision of the 1924 key and embodies no fundamental changes there is no need to analyse it separately, other than to say that Oudemans' (39) corrections concerning clauses F. 1. and F. 2. are quite necessary in order to prevent such errors as Vitzthum (50) made when he placed *Acarus spinatarsus* in the genus *Rhizoglyphus* instead of *Caloglyphus*. One of the chief weaknesses of the two keys, which will be more evident when we come to discuss the morphological relationships of the group, is that they mask to a certain extent the true relationships of the three principal groups. From these morphological studies it will be evident that the Acaridae (Tyroglyphidae) constitutes a single natural group and that its internal relationships, as well as its status in the Order Acari, would be better expressed by reducing the families Tyrophagidae, Tyroglyphidae, and Rhizoglyphidae to the status of tribes. A similar but very minor change that might be desirable would be to exchange clauses F. 1. and F. 2. since the Tyrophagidae are believed to be more primitive and should therefore be placed first. As a further result of the above-mentioned studies, certain exceptions will have to be made to the list of genera that Oudemans included in his family Tyroglyphidae. This necessitates the removal of the genera *Caloglyphus*, *Ceroglyphus*, *Froriepia*, *Histiogaster*, *Olafsenia*, and *Suidasia*. Oudemans (27) has aided us in this respect by erecting a family for the genus *Olafsenia* Oudms. 1924. This latter is a genus that he established (34) to accommodate *Tyroglyphus trifolius* Oudms. 1901, a mite with three peculiar spoon-like structures on the distal ends of the tarsi. As will be demonstrated later (p. 148), the genera *Caloglyphus*, *Ceroglyphus*, and *Histiogaster* show much closer affinities with the "tribe Rhizoglyphini," and should be included in it. This leaves only the genera *Froriepia* and *Suidasia* to be accounted for. Since the former of these is based on the hypopial stage, it is impossible, in our present state of knowledge, to classify it any more accurately than to say that it belongs to the "tribe Acaridini." The latter, an equivocal transitional form between the families Tyroglyphidae, Glycyphagidae, and Pterolichaeae, should be excluded, on the grounds of definition, from the Tyroglyphidae because the males possess neither anal nor tarsal suckers.

The third criticism of the above keys is of a more practical nature and concerns the use of the nuchal (33) or cervical (37) hairs as characters for separating the families Tyroglyphidae and Tyrophagidae. The difficulty lies in the fact that it is well-nigh impossible to draw an arbitrary line separating the dorsal from the marginal faces of the propodosoma as these surfaces lose their independence and significance when the animal is rotated or distorted slightly, which is quite possible in a microscopic mount. In the system of classification presented at the end of this paper, this difficulty has been overcome by choosing other characters to separate the groups in question.

In Oudemans' last great work on the Acaridae (39) he demonstrated very nicely his peculiar habit of characterizing higher taxonomic units on the basis of a single, freely selected character, which may vary. In this paper he erected a family for the genus *Caloglyphus* Berl. 1923 and decided to reclassify the

whole family on the basis of the nature of the male anal copulatory suckers*. He said that these structures are of two kinds: "1st, hemispherical structures raised above the level of the integument; 2nd, cup-shaped (finger-shaped 'napvormige') and surrounded by a more or less broad membranous ring." In the first group he placed his new family Caloglyphidae with its 10 genera: *Histiogaster* Berl. 1883, *Monieziella* Berl. 1897, *Mycetoglyphus* Oudms. 1932, *Caloglyphus* Berl. 1923, *Cosmoglyphus* Oudms. 1932, *Ceroglyphus* Vitz. 1919, *Suidasia* Oudms. 1905, *Rhizoglyphus* Clap. 1869, *Tyroborus* Oudms. 1924, and *Lardoglyphus* Oudms. 1927; many of these (with the possible exceptions of two new families) were formerly in the family Tyroglyphidae. The last mentioned family was left with a single genus of three species and was placed in the second group along with some unrelated families such as Psoroptidae, Gliricolae, Avicolae, Insecticolae (*Photia* Oudms. 1904), and the genera *Nanacarus* Oudms. 1902, and *Pontoppidania* Oudms. 1923 of the Detriticolae.

As a result of this highly artificial and unstable system, which apparently is Oudemans' last contribution to the subject, the genus *Tyroborus* loses its place in the Tyrophagidae and *Rhizoglyphus* in the Rhizoglyphidae. Several genera are placed close to the genus *Caloglyphus* whereas their relationship would be more accurately expressed if they were placed in a separate tribe Rhizoglyphini along with the genus *Rhizoglyphus*. Also, no mention is made of the genera *Stereoglyphus* and *Valmontia* of the 1924 family Tyroglyphidae, nor of the family Tyrophagidae and the rest of the family Rhizoglyphidae.

Sig Thor.—Adhering rather closely to Oudemans' 1924 and 1927 classification, Sig Thor (43, 44) divided his evolutionary tree into two branches of ascending complexity, which correspond to the families Tyroglyphidae, and Rhizoglyphidae. The former of these includes the 14 genera: *Tyroglyphiles* Pamp., *Tyroglyphus* Latr., *Tyroglyphopsis* Vitz., *Riemia* Oudms., *Monieziella* Berl., *Histiogaster* Berl., *Suidasia* Oudms., *Valmontia* Oudms., *Froriepia* Vitz., *Ceroglyphus* Vitz., *Caloglyphus* Berl., *Eberhardia* Oudms., *Olafsenia* Oudms., and *Coelognathus* Hss. in the main line of ascent, and two, viz., *Saproglyphus* Berl., and *Scatoglyphus* Berl., in a lateral offshoot. The family Rhizoglyphidae on the other hand has only seven genera: *Stereoglyphus* Berl., *Rhizoglyphus* Clap., *Schwiebea* Oudms., *Garsaultia* Oudms., *Sancassania* Oudms. (*Heteroglyphus* Foa), and *Acaridina* van Ben. in the family proper, and five, viz., *Tyrolichus* Oudms., *Tyroborus* Oudms., *Tyrophagus* Oudms., *Povelsenia* Oudms., and *Ebertia* Oudms., in a collateral but somewhat distant branch of the family.

Inasmuch as Sig Thor patterned his classification after that of Oudemans, the criticisms that were made of the inclusion of certain rhizoglyphid-like genera in the family Tyroglyphidae are applicable here. Furthermore, it is

* Apparently there must have been some doubt in Oudemans' mind about the validity of these characters, for on page 356 of the above-mentioned work, he says: "Hence we cannot assume without ado, that genera without anal suctorial cups are related and the same must be said for those who possess them." And farther down the same page, "The last three mentioned genera (viz., *Tyroglyphus* Latr. 1795, *Nanacarus* Oudms. 1902, and *Pontoppidania* Oudms. 1923), therefore, take a special place in the midst of the other Detriticolae, to which some genera without anal suctorial cups also belong. Yet, they are not directly related to each other! This gives cause for thought!"

rather difficult to understand why Sig Thor, using these keys, should associate the Tyrophagidae with the Rhizoglyphidae, as their relationship is not at all close. The former are thin-legged, delicate creatures, exhibiting no sexual dimorphism, whereas the latter are just the opposite.

Vitzthum.—Vitzthum's article on the terrestrial Acari published in *Tierwelt Mitteleuropas* (48) is very interesting and useful* in that it presents what might be called a summary of Oudemans' work prior to 1932, and shows how his keys may be adapted. Following the Dutch author's example, Vitzthum split the suborder Sarcoptiformes Reuter 1909 into two supercohorts, the Acaridae Latr. 1806, and the Oribatei Dug. 1834. The former of these was again subdivided into the three cohorts, Diacotricha** Oudms. 1906, Monacotricha Oudms. 1906, and Anacotricha Oudms. 1906, on the basis of the number of vertical hairs. The first of these is by far the largest group and includes 19 families, only three of which concern us here: viz., the Tyroglyphidae Donn. 1868 with three genera: *Histiogaster*, *Tyroglyphus*, and *Caloglyphus*; the Rhizoglyphidae Oudms. 1923 with two genera: *Rhizoglyphus* and *Schwiebea*; and the Tyrophagidae Oudms. 1924 with three genera: *Tyrolichus*, *Tyroborus*, *Tyrophagus*.

In the 1931 (49) classification the "Kohorte Diacotricha" was again by far the largest group, with 27 families, only four of which concern this discussion: the Tyroglyphidae*** with 13 genera and 40 species, the Rhizoglyphidae† with four genera and 10 species, the Ebertiidae†† with one genus with one species, and the Tyrophagidae††† with four genera and 15 species.

The only criticisms that can be made of these two systems are those that were made of Oudemans', viz., (i) the relationships would be better expressed if the groups Tyroglyphidae, Tyrophagidae, and Rhizoglyphidae were demoted to the rank of tribes in a family Acaridae (Tyroglyphidae); (ii) the Tyrophagini and Tyroglyphini should be placed together in the subfamily Acari-dinae; (iii) the genus *Caloglyphus* should be given tribal rank and associated with the tribe Rhizoglyphini in a subfamily Rhizoglyphinae.

Zakhvatkin.—Convinced that the system of classification advanced by Oudemans and accepted by most modern authors is quite artificial, the Russian zoologist, A. A. Zakhvatkin, set out to publish a series of studies on

* It is especially useful for us because it excludes exotic and tropical forms and treats of a geographical area somewhat similar to North America.

** The reader might note the difference in spelling. In his original descriptions Oudemans spelt this word *Diacotricha*. Later he used the form *Diacotricha*, which spelling Vitzthum seems to have followed.

*** In this family Vitzthum includes the following genera, some based on hypopial forms, others on tropical species. *Stereoglyphus* Berl., *Histiogaster* Berl., *Monieziella* Berl., *Valmontia* Oudms., *Tyroglyphus* Latr., *Acotyledon* Oudms., *Caloglyphus* Berl., *Achropodophorus* R.C. (= *Rhizoglyphus* Clap.), *Ceroglyphus* Vitz., *Suidasia* Oudms., *Froriepia* Vitz., *Tyroglyphopsis* Vitz., and *Videbantia* Oudms.

† This family includes the following genera: *Rhizoglyphus* Clap., *Schwiebea* Oudms., *Garsaultia* Oudms., and *Sancassania* Oudms.

†† This family has but a single genus, the *Ebertia* Oudms.

††† This family includes the following genera: *Tyrolichus* Oudms., *Tyroborus* Oudms., *Tyrophagus* Oudms., and *Povelsenia* Oudms.

the systematics of the mites of the family Tyroglyphidae. The first of these, appearing in 1937 (51), dealt briefly and in a general manner with the systematics of the whole family and extensively with the group Caloglyphini; the second, published in 1940 (52) was a *Key to mites injuring stores of agricultural products in U.S.S.R.* According to the scheme outlined in the first paper, the family Tyroglyphidae is divided into two subfamilies, the Tyroglyphinae (Oudms.) A. Z. and the Rhizoglyphinae (Oudms.) A. Z. The former of these is further subdivided into the two tribes, Tyroglyphini A. Z., with the single genus *Tyroglyphus*; and Tyrophagini A. Z., with the six genera *Tyrophagus*, *Tyrolichus*, *Tyroborus*, *Povelsenia*, *?Mycetoglyphus* Oudms. 1932, and *Aleuroglyphus* A. Z., 1940. The subfamily Rhizoglyphinae likewise is composed of two tribes, viz., the Rhizoglyphini A. Z., with the four genera: *Rhizoglyphus*, *Schwiebea*, *Histiogaster*, and *Thyreophagus*; and the Caloglyphini A. Z., also with four genera: *Caloglyphus*, *Isoglyphus*, *Eberhardia*, and *Cosmoglyphus*.

In the light of the morphological studies to be presented below, and because Zakhvatkin's system is the most recent and hence has the advantage of its predecessors in the possession of additional knowledge, it appears to be the most satisfactory yet devised for demonstrating the relationships in the family. Accordingly, it will form the basis for the systems of classification used in this paper. A few slight changes, however, of a logomachic rather than a zoological nature should be made. Ewing and Nesbitt (10) have pointed out that the accepted family name Tyroglyphidae, based on the genus *Tyroglyphus*, established by Latreille in 1796, as monotypical with *Acarus siro* Linnaeus as type, will have to be abandoned as it is synonymous with *Acarus* Linnaeus. Hence the family name should be changed to Acaridae and the tribal name to Acaridini.

Comparative Morphological Studies

CONCERNING THE BASIC STRUCTURE OF ACARID MITES AND TERMS TO BE EMPLOYED IN THE FOLLOWING DISCUSSIONS

Structurally, the acarid mites are as simple as any yet found. The suppression of segmentation and the fusion of the body into a compact mass have obliterated the prosoma and opisthosoma of generalized arachnids, separated the body into two false sections by the dorsal sulcus, and rendered the delimitation of the various regions of the body rather difficult. Vitzthum (47) and several other modern authors have divided the body into four arbitrary sections, gnathosoma, propodosoma, metapodosoma, and opisthosoma*, which are very convenient for mapping the position of the setae but which give rise to an erroneous idea about the relationship of the various parts. Whilst for the sake of convenience these terms will be used in this

* Several writers have adopted the following notation, which does not appear to be necessary though it is here presented for the sake of clarity.

Gnathosoma				
Propodosoma	} Podosoma	} Prosoma	} Idiosoma	} Proterosoma
Metapodosoma				
Opisthosoma				
				} Hysterosoma

paper it should be pointed out that I do not agree with the limits that Vitzthum has adopted for the various sections. He states that the metapodosoma is that region of the body that lies between the dorsal sulcus and pseudo-epimera and a line drawn behind the coxae of the fourth pair of legs. The separation of the propodosoma from the metapodosoma by the dorsal sulcus is an artificial division because this line is not a true suture between two parts of the primitive body but is an apodeme for the insertion of muscles. Embryological and comparative anatomical studies indicate that the four pairs of walking legs come from consecutive segments and belong to that portion of the body that is the prosoma in generalized arachnids. The fact that there is a dorsal sulcus and that the anterior and posterior legs exhibit slightly different types of setae and face different directions does not, in my opinion, indicate that the walking legs arise from fundamentally different parts of the body but that these differences are functional adaptations. Thus, when Vitzthum says that the dorsal sulcus is the anterior limit of the metapodosoma, it should be remembered that this is only an artificial line and not the front margin of a true section. Furthermore the insertion of the fourth coxal muscles indicates that dorsally the posterior margin of the metapodosoma should be just posterior of the third lumbar seta (7). Ventrally its posterior margin should be behind the fourth pair of coxae and in front of the genital pore.

When Vitzthum speaks of the opisthosoma he includes all that region of the body that lies posterior of an imaginary line drawn behind the last pair of legs. According to this definition the genital orifice and its external apparatus would be placed in the metapodosoma. As it has been shown above that the metapodosoma is only a term of convenience for the posterior part of the prosoma, and as the genital pore is on the second opisthosomatic segment of generalized arachnids, I have included it in the opisthosoma. The fact that it lies between the coxae of the fourth pair of legs is easily explained by the assumption that in an animal like a mite where there has been so much condensation and telescoping of segments the coxae are pushed laterally and backward to accommodate their muscles until they have come to occupy a place somewhat posterior of their primitive position. At the same time, the genital orifice has been pushed slightly forward. Thus, the opisthosoma as understood in this paper is that part of the body that is behind the third lumbar setae (7) and the posterior margins of the coxae of the fourth pair of legs. Between the fourth pair of legs it extends forward in a tongue-like structure to include the genital orifice.

Gnathosoma (see Fig. 1).—The gnathosoma is the most inconspicuous part of the body, lying as it does, partially hidden in a shallow anteroventral depression of the overhanging propodosoma. It arises from the first two postoral segments of the body and develops into the mouth parts. The epistome is wanting or so reduced as to be vestigial. The chelicerae are massive, shear-like structures provided with teeth. The pedipalps are three-jointed and usually bear a small seta on the lateral face of each joint. The terminal joint carries a little tubercle that may be either a sense organ or a

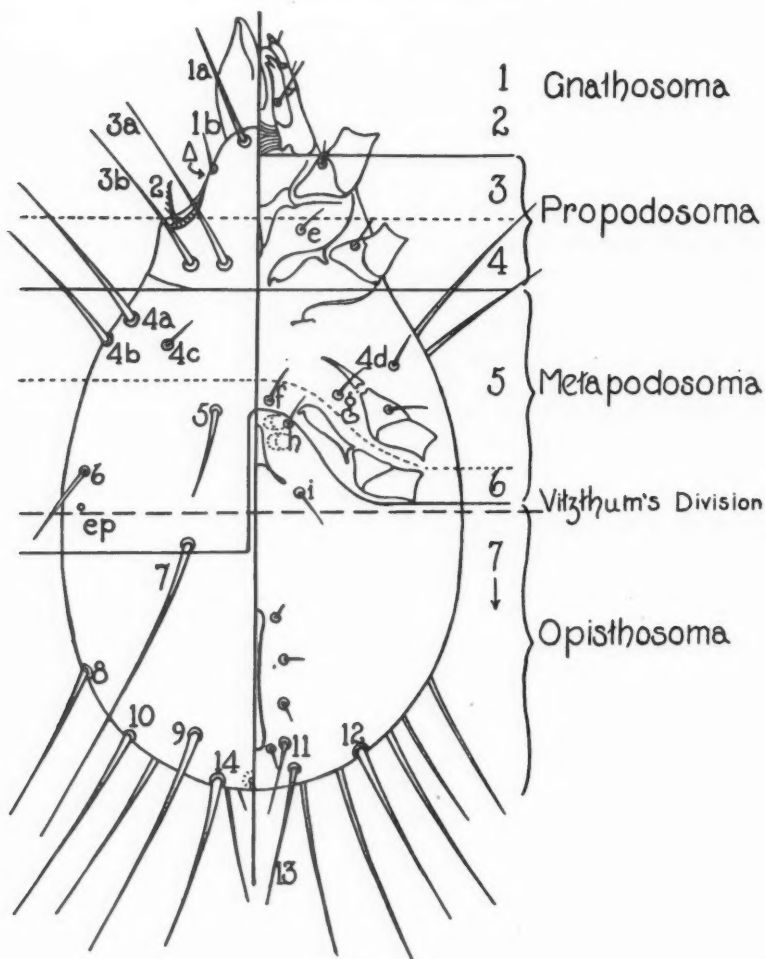


FIG. 1. A conventionalized sketch of an acarid mite showing the approximate position of the setae; the left side shows the setae of the dorsal surface, the right those of the ventral surface. For the sake of simplicity the legs have been cut off after the femoral segment.

Names of setae and Oudemans' equivalents are: 1. Rostral—s[eta] vert[icis] int[ernis]; 1b. Cervical bristles—s[eta] vert[icis] ext[ernis]. 3a. Inner propodosomatic—s[eta] scap[ularis] int[ernis]. 3b. Outer propodosomatic—s[eta] scap[ularis] ext[ernis]. 4c. Inner humeral—d₁. 4a. Middle humeral—s[eta] hum[eralis] int[ernis]. 4b. Outer humeral—s[eta] hum[eralis] ext[ernis]. 5. First lumbar—d₂. 6. Second lumbar—s[eta] lumb[alis] anterioris. 7. Third lumbar—d₃. 8. Outer submarginal—s[eta] lumb[alis] posterioris. 9. Inner submarginal—d₄. 10. Middle submarginal—s[eta] sacr[alis] ext[ernis]. 14. Marginal—s[eta] sacr[alis] int[ernis]. Setae for which Oudemans gives no equivalent names: 2. Pseudostigmatic organ. 11. Anterior postanal. 12. Ventral submarginal. 13. Posterior postanal. Δ. Grandjean's organ [= nuchal bristle]. Ep. Excretory pore or opening of so-called "oil gland." 4d. Inferior humeral.

modified fourth joint. The pedipalpal coxae or gnathobases bear distally a lacinia-like prolongation with two large teeth. Ventrally and mesially they are covered by a flexible membrane that is fused in the mid-line to form the hypostome. The anterior extension of the lower body wall acts as a labium and has two large setae.

Propodosoma.—The propodosoma is that region of the body that develops from the third and fourth postoral segments and that, in the post-embryonic stages, lies between the base of the mouth parts and the dorsal sulcus and pseudo-epimera. Anterodorsally it is covered by a mildly sclerotized plate, the "propodosomatic shield," which in favourable light usually appears shagreened. The third segment, or the first section of the propodosoma, bears the first pair of walking legs, a pair of strong rostral setae (1a*), Grandjean's (14) organ**, a pair of cervical bristles (1b), and a pair of feather-like or smooth pseudostigmatic organs (2) that arise from the dorsal surface of the coxae of the first pair of legs. The fourth segment, or second part of the propodosoma, bears the second pair of walking legs, two pairs of propodosomatic setae, the inner (3a) and outer (3b), and on the ventral surface a pair of minute anterior interepimeral bristles (e).

Metapodosoma.—The metapodosoma is derived from the fifth and sixth postoral segments. The fifth segment bears on the dorsal surface just posterior of the dorsal sulcus an irregular transverse row of setae, the inner (4c), the middle (4a), and the outer (4b), humeral setae; on the ventral surface are found the third pair of legs and a small pair of inferior humeral setae (4d) just behind the pseudo-epimera. The sixth segment has three pairs of dorsal setae, the first lumbar (5) close to the mid-line, the second lumbar (6) just anterior of the excretory gland, and the third lumbar (7) slightly posterad of the latter and close to the mid-line; ventrally it bears the fourth pair of legs, the posterior interepimeral bristles (g) between epimera III and IV and the anterior paragenital bristles (f) between the median tips of the fourth epimera.

Opisthosoma.—The opisthosoma bears five pairs of major setae. Four of these, the outer submarginal (8), inner submarginal (9), middle submarginal (10), and marginal setae (14) arise from the dorsal surface or margin; the fifth pair, the ventral submarginal (12), spring from the ventral surface near the hind border. Close to these and posterior to the anus are to be found two pairs of setae of varying lengths. These are known as the anterior (11) and posterior (13) postanal setae. Surrounding the female anal cleft are four pairs of little anal bristles. In the male they are replaced by a pair of copulatory suckers and, anterior to them, a pair of male anal bristles. In the female, the ventral surface of the opisthosoma bears the genital orifice, two pairs of

* The italic number in parentheses after a name refers to Fig. 1. Throughout the paper the term "setae" will be reserved for long flexible hairs and "bristles" for short rigid structures.

** Grandjean's organ is a structure that arises from the lateral side of the body (neck region) just anterior of the base of the first coxae. In the Acarinae it is a tiny tree or root-like structure closely appressed against the side of the body. In the Rhizoglyphinae it has become modified as a large horn-like process that extends obliquely out from the body and that is readily visible in dorsal and ventral mounts.

genital suckers, and two pairs of *paragenital bristles*, the *middle (h)*, and the *posterior (i)*. On the dorsal surface near the posterior end is to be found a minute pore with puckered lips, the opening of the bursa copulatrix. With the substitution of a penis and a penis carrier for the female genital orifice, the same structures and bristles are found in the male as in the female.

Tarsi.—The legs of acarid mites are considerably more complex and specialized than any other part of the body. Whilst maintaining a fundamental plan of organization, they exhibit sufficient modification to indicate the evolutionary trends of the group. For that reason a study of tarsal chaetotaxy is very useful in tracing the relationships in the family. As was mentioned above, the necessities of locomotion have directed the two anterior pairs of legs forwards and the two posterior backwards. Not only may the legs be separated in this manner but they may also be differentiated by the number, type, and disposition of the spines that they bear. This difference is nowhere more noticeable than on the tarsi where there is a progressive simplification in the type of setae as one passes from the first to the fourth legs: i.e., the first tarsus carries a full complement of setae, the second shows some simplification with respect to the sensory setae, and the third and fourth are entirely devoid of such organs. If we accept the theory that states that the microsense, macrosense, and sub-basal setae (*vide infra*) are sensory organs, this disappearance is not surprising for sensory structures are commonly found at the anterior end of animals.

Tarsus I (see Fig. 2).—For convenience the setae on the tarsus of the first leg may be separated into three clusters, a proximal, median, and distal group. Those of the proximal group are all arranged on the dorsal and lateral faces of the tarsus, and include the following: a large dorsal organ of velvety appearance, the *macrosense* seta; at its base a tiny spine, the *microsense* seta; dorsally but more distally, the *postdorsal median* seta; and on the lateral face a little peg-like organ, the *sub-basal* seta, which is reputed to have a sensory function. In some species the postdorsal median seta has migrated laterally to take up a position beside the sub-basal seta. When it occupies such a position it is called the parasub-basal seta. The setae of the median group are arranged in a whorl about the middle of the tarsus. From the dorsal face arises the *dorsal median* seta, from the lateral face, the *lateral median* seta, from the mesial face, the *mesial median* seta, and from the ventral face the *ventral median* seta. The distal group of setae may be further separated into a dorsal and a ventral cluster. The ventral cluster is composed of from three to five little spinules: one *ventral terminal spinule*; two *inner ventral terminal spinules* (a mesial and lateral one); and two *outer ventral terminal spinules* (a mesial and a lateral one). The dorsal cluster is composed of four quite long hair-like setae (longest on tarsus). Three are located on the dorsal face, the *first dorsal terminal* seta, the *second dorsal terminal* seta, and the *caruncular seta*. One is located on the mesial face, the *mesial terminal* seta. The terminal claw is supported by, and articulates on, two supporting

rami. Its base is covered by a thin membrane that may be distended as a caruncle.

Tarsus II.—The tarsus of the second leg is similar to that of the first except that it has been somewhat simplified in the basal region by a reduction in the number of its setae. The parasub-basal, sub-basal, and microsense setae are missing from the proximal group, leaving only the macrosense seta, which

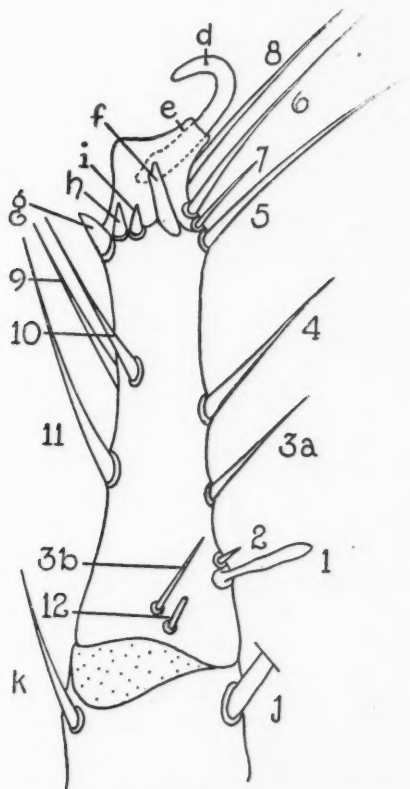


FIG. 2. Conventionalized view of the first tarsus of an acarid mite.

1. Macrosense seta. 2. Microsense seta. 3 (a). Postdorsal median seta. 3 (b). Parasub-basal seta. 4. Dorsal median seta. 5. First dorsal terminal seta. 6. Caruncular seta. 7. Second dorsal terminal seta. 8. Mesial terminal seta. 9. Mesial median seta. 10. Lateral median seta. 11. Ventral median seta. 12. Sub-basal seta. d. Claw. e. Caruncle. f. Supporting ramus of claw. g. Ventral terminal spine. h. Outer ventral terminal spinule. i. Inner ventral terminal spinule. j. Dorsal tibial spine. k. Ventral tibial spine.

as a result becomes quite conspicuous. In the median group all the setae are present whilst in the distal group all may be found except the caruncular. It might be added in passing that those setae of the median group, which in

some species take up a distal position and assume falcate ends, behave as they do on the first tarsus (*vide infra*).

Tarsus III.—The simplifications begun on Tarsus II are carried still further on the third and fourth legs with the result that it is difficult to homologize the setae on these members with those of the first two. It may be stated, however, that on the third tarsus, none of the setae of the proximal group is present. The median group is represented by a ventral and a mesial seta. The distal group has only the first and second dorsal terminal setae and an anomalous lateral seta. In so far as the mesial median seta is distally placed in the females of many caloglyphid mites, it is possible that the "anomalous" lateral seta is the missing lateral seta of the median group. If this interpretation is correct, the median group would lack only the dorsal median spine, and the distal group the mesial, and caruncular setae. When the males of some rhizoglyphid mites assume the heteromorphic form, the third leg changes from the typical female shape to a short heavy structure that terminates in a large claw bearing all the setae of the normal tarsus but in a very compact arrangement.

Tarsus IV.—In all typical acarid mites the fourth tarsus assumes two different forms depending on the sex of the individual. In the female it is almost identical with the third tarsus; thus the description given above for that member may be applied here except that in caloglyphid females the mesial median spine never leaves the median position. The fourth tarsus of the male is characterized by two large copulatory suckers. As in the female, there are no proximal and only two median setae. The distal group is represented by a single seta, which appears to be the first dorsal terminal seta. The possession of a single seta in this position would indicate that the other two setae, viz., the lateral and second dorsal terminal setae of the female, have been lost or modified. Grandjean has proposed a theory to account for this loss. He believes that the suckers are homologous with the terminal setae of the female because the cores of the suckers and the setae are both composed of actinochitin and thus have arisen from the same primitive "anlagen." To test these claims, I examined the tarsi with polarized light and found that the structures behaved as the French author claimed they should: i.e., all the spines and a very minute centre peg in the "lid" of the suckers glowed with the brilliancy characteristic of actinochitin when so examined.

There are certain difficulties, however, which would place this theory in abeyance until some suitable solution could be found. The most important of these are: (i) the homologous structures are too widely separated in the male and female to have been derived from the same source; (ii) the portion of actinochitin in the suckers is far less than would be expected if they were homologous with the setae.

TARSAL CHAETOTAXY

From the above descriptions it is quite evident that there are only two types of tarsi, characteristic, respectively, of the two anterior and the two posterior pairs of legs. As the first and fourth tarsi are the more representative members of each group, and are more diagnostic of the various species studied, they alone will be described in the following chaetotactic studies.

TARSUS I (Figs. 4 to 15)

The Setae of the Proximal Group

Using Oudemans' concept (35) that the genus *Tyrophagus* represents one of the most primitive genera in the family Acaridae, the tarsi of representative species may be arranged in a sequence to show their advance in complexity. Thus it is not surprising to note that in *Tyrophagus putrescentiae* (Schr.) (Fig. 4), *Tyrophagus dimidiatus* var. *dimidiatus* (Herm.), and *Tyrophagus infestans* (Berl.) (Fig. 5), the postdorsal median seta (3) remains in its primitive position, on the dorsal face of the tarsus between the microsense seta (2) and the dorsal median spine (4). The sub-basal (12) and microsense seta (2) likewise retain their primitive positions and size. The macrosense seta (1), in *T. infestans* (Fig. 5), assumes a long rod-like shape whilst in the other two species mentioned it is mildly clavate.

The postdorsal median seta (3) in *Acarus siro* L. (Fig. 6), *Aleuroglyphus ovatus* (Troup.) (Fig. 7), *Eberhardia pedispinifer* Nes. (Fig. 8), *Caloglyphus spinitarsus* (Herm.) (Fig. 9), *C. longitarsus* (Banks) (Fig. 10), and *Rhizoglyphus rotundatus* Nes. (Fig. 11) has moved obliquely down the tarsus to take up a position close to the sub-basal seta (12). To prevent nomenclatural confusion it has been renamed "the parasub-basal seta" (3) when it occupies this position. In the first five species mentioned it is a thin hair-like structure, whereas, in the sixth, *R. rotundatus*, it is a stout conical-shaped spine. The macrosense and microsense setae arise from separate setae pits in *Acarus siro* and *Aleuroglyphus ovatus* whilst in all the Rhizoglyphinae they spring from a single oval-shaped membranous cushion. As may be seen from the figures the macrosense seta in all these forms is slightly clavate.

Rhizoglyphus echinopus (F. & R.) (Fig. 12), *Schwiebia talpa* Oudms. (Fig. 13*) *Histiogaster carpio* (Kramer) (Fig. 14), and *Thyreophagus angusta* (Bks.) (Fig. 15) exhibit a further stage of development in that the parasub-basal sense seta (3) has disappeared entirely. All the other structures of the proximal group appear to be normal except the macrosense seta of *T. angusta*, which is quite long, i.e., almost as long as the tarsus itself.

The Setae of the Median Group

The setae of the median group show considerable modifications. In

* Fig. 13. This figure was borrowed from Vitzthum (47), because I have never seen a preparation of this rare continental species. Vitzthum says that it possesses an opisthosomatic shield and that in his opinion it has frequently been confused with *R. echinopus* to which it bears a striking resemblance. Since the drawing represents the mesial face of the second tarsus, neither the micro-sense seta nor the parasub-basal seta is shown.

Tyrophagus putrescentiae (Fig. 4), *T. infestans* (Fig. 5), *Acarus siro* (Fig. 6), *Aleuroglyphus ovatus* (Fig. 7), and *E. pedispinifer* (Fig. 8), they retain their primitive position and nature, though in the last two mentioned species, the mesial (9) and lateral (10) median setae have begun to move distally, foreshadowing the changes to be mentioned shortly. In all the Rhizoglyphinae, the lateral (10) and the mesial (9) median setae have migrated distally until they arise just proximad of the base of the ventral terminal setae, and are modified as long whip-like hairs that may or may not bear distal paddle-like dilatations. In *C. spinitarsus* (Fig. 9) and *C. longitarsus* (Fig. 10) the distal dilatations of the lateral and mesial setae are leaf-shaped; in *R. rotundatus* (Fig. 11) modified crescents; and in *R. echinopus* (Fig. 12) decided crescents. The mesial seta is reduced considerably in size in *R. echinopus*. Vitzthum represents these setae in *S. talpa* (Fig. 13), as unmodified whip-like structures similar to those found in *H. carpio* (Fig. 14). *Thyreophagus angusta* (Fig. 15) has retained a pattern very similar to that found in *Acarus siro*, in that the lateral and mesial median setae are simple unmodified structures arising from a position relatively close to the primitive one.

The dorsal median seta (4) undergoes considerable change. In *Tyrophagus putrescentiae* (Fig. 4), *Tyrophagus infestans* (Fig. 5), and *Acarus siro* (Fig. 6), it is primitive in shape and position. In *Aleuroglyphus ovatus* (Fig. 7) and *E. pedispinifer* (Fig. 8), however, the differential shortening of the tarsus has resulted in its moving proximally to occupy a position relatively closer to the microsense seta, an adumbration of the state to be found in the Rhizoglyphinae. As further confirmation of this trend, the dorsal median seta in the last two mentioned species has begun to assume the spine-like form of the Rhizoglyphinae. In *C. spinitarsus* (Fig. 9) it is a slight spine whilst in *C. longitarsus* (Fig. 10) it is a decided spine reminiscent of the Rhizoglyphini. The tendency that the dorsal median seta has to increase in size and to approximate the microsense seta is completed in *R. rotundatus* (Fig. 11), *R. echinopus* (Fig. 12), and *S. talpa* (Fig. 13), where it becomes a large thorn-like structure placed immediately distad of the microsense seta. In *H. carpio* (Fig. 14), it retains the same position and shape but is relatively smaller. *Thyreophagus angusta* (Fig. 15) is again somewhat out of the direct line of descent in that the dorsal median seta is slightly removed distally from the base of the microsense seta and has taken a peculiar rod-like shape.

The ventral median seta retains the primitive position in all the forms studied, and the primitive thin hair-shape in the Acarinae and *Thyreophagus*. In the Rhizoglyphinae it becomes relatively more thorn-like as we progress through the series until it becomes quite huge in *S. talpa* (Fig. 13). The shortening of the tarsus in *R. echinopus* and *S. talpa* has brought it into what appears to be a distal position.

The Setae of the Terminal Group

The setae of the terminal group may be separated for convenience into two divisions, a dorsal and a ventral cluster. The spines of the ventral group show

very little modification. In the female of *Acarus siro* (Fig. 6) the ventral spinule is quite large; the mesial and lateral inner and outer terminal spinules are present. In the male of the same species (not figured) the ventral terminal spinule is reduced to a mere bristle-like seta and the two outer terminal spinules have fused to form a large spine comparable with, if not larger than, the ventral terminal spinule of the female. The three most ventral spinules, i.e., the ventral, mesial, and lateral outer terminal spinules, reach their maximum development in *Aleuroglyphus ovatus* (Fig. 7) where they are relatively large. The mesial and lateral inner terminal spinules, however, are missing. This arrangement is also found in *S. talpa*. Apart from these differences there is little further modification, and, as all the species are adequately figured, there is no need to describe them further.

In the dorsal group, the first dorsal terminal seta (5) remains in relatively the same position throughout the entire series of species studied, and in some of the Rhizoglyphinae, such as *C. spinilarsus*, *C. longitarsus*, *R. rotundatus*, and *R. echinopus*, its distal end is dilated in the form of a narrow paddle. In all others it remains a simple hair.

The second dorsal terminal seta (7) is represented by a slight hair-like structure in the primitive species *Tyrophagus putrescentiae*, *T. infestans*, and *Acarus siro*. While remaining in the primitive position in *Aleuroglyphus ovatus*, it becomes much coarser and spine-like. As a small peg-like spine, it foreshadows the trend of the series by taking up a new position in *E. pedispinifer* at the dorsolateral corner of the tarsus and pushing the first dorsal terminal seta (5) into a proximal position. In *C. spinilarsus* it becomes a large thorn-like structure that is the end form and characteristic of the rest of the series.

The caruncular seta (6), as the name would imply, arises from the caruncle. In *T. putrescentiae*, *T. infestans*, *Acarus siro*, and *Aleuroglyphus ovatus*, it is one of the larger, well developed setae. In the Rhizoglyphinae it appears* to move from the dorsal to the mesial face of the caruncle and assumes a shape characteristic of this family.

The last of the tarsal setae to be discussed is the mesial terminal seta (8), which arises from the mesial face of the tarsus close to the base of the supporting ramus of the claw. It retains this primitive position and the shape of a hair in *T. putrescentiae*, *T. infestans*, *Acarus siro*, *Aleuroglyphus ovatus*, and *E. pedispinifer*. In *C. spinilarsus*, *C. longitarsus*, and *H. carpio*, it is reduced to a short stout spine that arises from a position slightly more proximad of the ramus than in the preceding species. *R. echinopus*, *S. talpa*, and *Thyreophagus angusta* revert to a condition very similar to that found in the more primitive species: i.e., the mesial seta becomes long again and in *R. echinopus* it bears a falcate end.

* The phrase "appears to" is used here advisedly because, owing to the billowy nature of the caruncle in the primitive types, it is impossible to say exactly from which face the caruncular seta arises.

TARSUS III (Figs. 26, 27, and 34)

Since as the third tarsus of both sexes is identical with the fourth tarsus of the female, no separate description will be given here other than for certain irregular forms. Fig. 34 represents the third tarsus of the female of *C. spinitarsus*. Compared with the fourth tarsus of the female (Fig. 33), or the third tarsus of the normal male (Fig. 26), it will be noted that one of the setae of the median group, viz., the mesial median seta, has moved distally to take up a position just proximad of the supporting ramus of the claw. This migration, with the resulting superficial resemblance of the terminal part of the third tarsus to either the first or the second tarsus, is a characteristic of the females of the genus *Caloglyphus* and of the males of a few of its species.

The third tarsus of the heteromorphic male of *Caloglyphus armipes* (Bks.)* is shown in Fig. 27. As it is very typical of that found in all such males, it may be used as the model for this discussion. Compared with Fig. 26, which shows the corresponding tarsus of a normal male, it is evident that a considerable rearrangement of the setae has taken place. From muscle insertions we know that the long terminal claw of Fig. 27 is homologous with the terminal claw shown in Fig. 26. Likewise the mesial thumb-like claw is homologous with the combined ventral terminal setae. Taking these two structures as the fixed points on which to establish homologies, it is logical to assume that the ventral (*b*) and mesial (*a*) median setae have moved distally with the shortening of the tarsus until they finally arise from the position shown in Fig. 27. This is not unusual because the mesial median seta of female caloglyphid mites does much the same thing. (A further proof of the possibility of this hypothesis is the fact that (*a*) in the heteromorphic male like the "distal" mesial seta of the female bears a falcate end.) The first dorsal terminal seta (*c*) of the normal male (Fig. 26) is represented by a similar seta in the heteromorphic form. The second dorsal seta (*e*) is reduced from a stout spine to a simple hair-like seta. The mesial terminal seta (*d*) remains in relatively the same position and has the same shape in both forms.

TARSUS IV FEMALE (Figs. 28 to 39)

Proximal Group

No setae of the proximal group are present (*vide supra*).

Median Group

The position and nature of the setae of the median group is constant throughout the series of forms studied. It is true that in the Rhizoglyphinae the setae become somewhat spiniform but as that is a general characteristic of the tarsal setae of this subfamily and of the genus *Rhizoglyphus* in particular, it is not extraordinary.

* Since the heteromorphic male of *C. spinitarsus* has not been found, that of *C. armipes* has been substituted for it and accordingly Fig. 27 has been drawn from this latter species. These two species, however, are so nearly identical that Fig. 26 might well represent the third leg of either.

Distal Group

As in the other tarsi, the ventral terminal setae show very little variation, other than that found in *Acarus siro*, where again, the most ventral spine of the ventral group is larger than in any of the others. The first and second dorsal terminal setae behave in much the same manner as they did on the first tarsus. The first remains a simple seta in all the forms studied, except *C. spinitarsus* and *C. longitarsus*, where the free end bears a falcate paddle. The second dorsal terminal seta progresses from a simple small seta in *Tyrophagus putrescentiae*, *T. infestans*, and *A. siro*, to a small conical-shaped spine in *Aleuroglyphus ovatus* and *E. pedispinifer*; continuing, it becomes a large thorn-like process of the tarsus in *C. spinitarsus* and the representatives of the Rhizoglyphini. The lateral terminal seta is another of the stable structures and shows little variation throughout the entire series. Usually placed close to the supporting ramus of the claw, it may move dorsally to arise from a position closer to the second dorsal terminal seta (spine) in *R. rotundatus* and *R. echinopus*. Typical of most of the members of the genus *Caloglyphus* its terminal end is falcate in *C. spinitarsus* and *C. longitarsus*.

Whilst not belonging to the tarsus, the dorsal seta of the tibia might be considered at this time. As may be seen from the figures it becomes progressively shorter in the more advanced members of the series. Thus in *T. putrescentiae*, *T. infestans*, and *Acarus siro*, it is longer than the tarsus, in *Aleuroglyphus ovatus* and *E. pedispinifer* almost as long, and in the remaining members about one-half the length.

TARSUS IV MALE (Figs. 16 to 25)

Proximal Group

No setae of the proximal group are present (*vide supra*).

Median Group

As the setae of the median groups show no greater modification than they do in the female, there is no necessity to discuss them here. For their shape and position on the tarsus, the reader is referred to Figs. 16 to 25.

Distal Group

The dorsal and ventral terminal setae are simple unmodified structures similar to those of the female. As was mentioned above, there is but a single dorsal terminal seta that sometimes is as long as, or longer than, the tarsus. Its free end may be falcate in the genus *Caloglyphus*.

The tarsal suckers are clasping devices used to hold the female in copulation. They have much the same form in all the males of the family Acaridae, and each is composed of three parts: a heavily sclerotized lid (of concentric rings of chitin) that fits flush into the wall of the tarsus (like a stove-lid); a membranous connection sleeve between it and the tarsus; and a slip of muscle inserted at the centre of the lid to bring about its contraction. I have not been able to determine whether, in action, the whole sucker contracts into the tarsal wall or whether only the shape of the lid is changed. As the latter is

cross-bow-shaped in cross-section, it is possible that its centre is depressed to produce the required suction. With some types of fixative, however, the whole lid is so firmly contracted that it is very difficult to distinguish it from the wall of the tarsus.

Whilst not changing much in shape, the position of the suckers varies considerably in the different genera. Unfortunately, however, there is no indication of any progressive pattern in the series. In *T. putrescentiae* (Fig. 16), they are so placed that they divide the tarsus into three equal parts. In *T. infestans* (Fig. 17), on the other hand, which belongs to the same genus but to a different grouping, the two suckers are located in the proximal third of the tarsus. *Acarus siro* (Fig. 18) follows somewhat the same plan though here the tarsus is shorter. In *Aleuroglyphus ovatus* the two suckers are placed fairly close to the two ends of the tarsus. The reverse of this is found in *E. pedispinifer*, which is similar to *T. putrescentiae* in that both suckers are placed closer to the middle of the tarsus. In *C. spininarsus* (Fig. 21), and *C. longitarsus* (Fig. 22), the suckers are located on the distal half of the segment. In both, the distal sucker is placed so close to the end that its membrane is almost confluent with the caruncle. In *R. rotundatus* (Fig. 23), the suckers are smaller and placed closer to the distal end. *R. echinopus* (Fig. 24) and *H. carpio* (Fig. 25) have large distinct suckers, placed less than one-half of their own diameter apart and close to the distal end of the tarsus. *S. talpa* (not figured) is very similar to *R. echinopus*. *Thyreophagus angusta* (not figured) appears to have only one sucker.

In concluding the discussion of the male tarsus, a short note should be added on the dorsal tibial seta. Like its homologue in the female, it becomes progressively shorter as more advanced types are examined. Thus we find that in *Tyrophagus putrescentiae*, *T. infestans*, and *Acarus siro*, it is longer than the tarsus; in *Aleuroglyphus ovatus*, *E. pedispinifer*, and *R. rotundatus*, it is almost as long as this segment; and in *C. spininarsus* and *C. longitarsus* it is only one-half of its length. In *R. echinopus* and *H. carpio* it is reduced to a short heavy thorn-like spine.

BODY CHAETOTAXY

In working out chaetotactic patterns it is necessary to have certain structures that are extremely stable and as such may be used as landmarks or fixed points in explaining the relationship of the variable setae. In these studies such structures were the pore of the excretory gland, and the rostral, outer propodosomatic, humeral, third lumbar, and inner submarginal setae. For convenience in description the setae of the body will be divided into three arbitrary groups, viz., those of the propodosoma, the metapodosoma, and the opisthosoma. (The names and positions of the setae are given in the general discussion, pp. 149 to 152).

Before beginning the description and making reference to the plates, it might be well to interject a few words of explanation. To conserve space only half of each surface of the specimen has been drawn: i.e., the left side

of the figure represents the dorsal, and the right side, the ventral face. Also, since the adult stages of some of the mites show remarkable similarity, only the more striking member of a similar pair is figured. Thus, *Tyrophagus putrescentiae*, *C. longitarsus*, and *S. talpa** are omitted in favour of *T. infestans*, *C. spinitarsus*, and *R. echinopus*, respectively. The stippling drawn over the epimera in the ventral views represents areas of sclerotized integument.

Setae of the Propodosoma

Again considering *T. putrescentiae* and *T. infestans* as the most primitive mites in our series, we may take the chaetotactic pattern of the latter (Figs. 40 and 41) as the initial point of our discussion. The rostral seta** (1a) is in the primitive position on the extreme anterior end of the propodosoma overhanging the chelicerae. The faintly pectinated cervical bristle (1b) arises from the dorsolateral margin of the body just anterior to the first trochanter. Ventral to it, on the lateral part of the "neck region" and closer to the base of the first trochanter is to be found Grandjean's organ. In this species it assumes the form of a tree-root in which there is one large dominant tap-root and two or three smaller ones. The pseudostigmatic organ (2) is thin and heavily pectinated on two sides, with the result that it looks like a feather. The inner propodosomatic seta (3a) is longer than the outer (3b) and both they and the rostral are pectinated.

Acarus siro (Figs. 42 and 43) exhibits a relatively similar arrangement. In the male (Fig. 42), but not in the female (Fig. 43), the cervical bristle is slightly more dorsal than in the species just described. Grandjean's organ is again root-like but here it is composed of two heavily branched roots of unequal size. The pseudostigmatic organ is plumper than in *T. infestans* and appears to have pectinations on all sides. The propodosomatic setae are of equal length, though occasionally the inner may be longer. Both sometimes bear slight pectinations as do the rostral setae.

The disposition of the setae on the propodosoma of *Aleuroglyphus ovatus* (Figs. 44 and 45), is, in all essential respects, similar to that of *Acarus siro*. There are two slight differences, however, that may be noted: viz., the inner propodosomatic seta is usually shorter than the outer; and in both sexes, the two setae are more heavily and distinctly pectinated.

As the first representative of the subfamily Rhizoglyphinae, *E. pedispinifer* (Figs. 46 and 47) exhibits certain changes in the nature and position of the propodosomatic setae that are characteristic of this group. (i) The cervical bristle (1b) has moved dorsally from its primitive place to take up a position close to the middle of the lateral border of the propodosomatic shield and has become shorter and peg-like. (ii) Grandjean's organ, in the form known in the Acarinae, has disappeared. In its place there has arisen a large horn-like

* Since Vitzthum (47) states that *R. echinopus* and *S. talpa* are identical except for the opisthosomatic shield of the latter, I did not think that it was necessary to borrow a figure from the German author's work as was done in the case of the first tarsus. Any person desiring to see either the figure or the description is referred to Vitzthum's paper.

** Because these animals are bilaterally symmetrical, and since I wish to prevent confusion, unless otherwise stated, or where the sense is obvious or continuity demands it, only one seta of each pair will be described: i.e., the description will be all in the singular.

process that is known as the nuchal bristle and that is believed to be homologous with it. Unlike its homologue in the Acarinae, where it is so thin that it appears to be nothing more than an etching on the integument, in the Rhizoglyphinae it is sufficiently large and free from the body to be readily visible in dorsal or ventral views. (iii) The inner propodosomatic seta is only about one-quarter as long as the outer. The rostral seta remains in its fixed position but assumes a sigmoid shape. The pseudostigmatic organ is fairly long but sparsely pectinated.

The changes initiated in *E. pedispinifer* are continued unmodified in *C. spinilarsus* (Figs. 48 and 49). The pseudostigmatic organ, however, is reduced to a tiny peg. This reduction in size is typical of many species of the genus *Caloglyphus*. In others it may retain the length found in the subfamily Acarinae but in few, if any, is it ever pectinated. The nuchal organ is slightly modified in that its tip is bifurcated. At the base of the pseudostigmatic organ, between it and the chitinous ridge that forms the lateral border of the propodosoma, is to be found a structure that appears to be a slit with very thick lips. While it is difficult to be dogmatic about such minute structures, it is probable that this is either the opening to a gland—similar to the supercoxal gland of the Oribatei—or a respiratory pore. Oudemans (39) favours the latter view, calls it a "parastigma," and maintains that he was able to see a trachea leading away from it. Hirst (16) and Grandjean (15) are of a similar mind and affirm that some of the Atracheata have respiratory systems. For the purposes of this paper this structure will be considered a vestigial stigma in view of the fact that it is commonly found in the Acaridae.

In both the representatives of the genus *Rhizoglyphus* shown, viz., *R. rotundatus* (Figs. 50 and 51) and *R. echinopus* (Figs. 52 and 53), the chaetotactic pattern is the same as in *C. spinilarsus*. The only slight change is that the inner propodosomatic setae are, if anything, shorter. In some species of the genus they have disappeared entirely, leaving only the seta pits to mark their position.

The propodosoma of *H. carpio* (Figs. 54 and 55) bears a superficial resemblance to that of *R. echinopus* but on closer examination it will be noted that all but the "fixed" setae have disappeared; i.e., there is no trace of either the cervical, or inner propodosomatic setae. The nuchal organ, however, remains and a very tiny pseudostigmatic organ can be seen.

Setae of the Metapodosoma

The setae of the metapodosoma may be divided into three groups; viz., the humeral setae, arranged in a partial whorl or band about the body just back of the dorsal sulcus; the lumbar setae, forming a rough quadrilateral figure on the lumbar flank of the body, with the pore of the excretory gland as one of its corners (the posterolateral); and three pairs of paragenital bristles, constituting a circlet about the genital opening. As these last mentioned setae vary so little from species to species, there is no need to discuss them, but only to refer the reader to the figures.

Some of the metapodosomatic setae of *Tyrophagus infestans* (Figs. 40 and 41) are quite short, while others show indications of the tendency that this species has for long setae. Thus, in the humeral group, we observe that the inner (4c) and inferior (4d) setae are bristle-like whereas the middle (4a) and outer (4b) are among the longest setae of the body and have a length equal to the width of the creature. The first and second lumbar setae are short. The third is one of the longest of the body. In the living state it is carried well arched up over the animal. Like the setae of the propodosoma and opisthosoma those of this region are pectinated.

The setae of the metapodosoma of *Acarus siro* (Figs. 42 and 43) are all short. In the humeral group, the outer is the only one that attains any size, being about one-half as long as the body is wide. It is also the only seta of this part of the body that, on rare occasions, shows slight pectinations. The lumbar setae are almost equal in length.

In length and disposition the setae of *Aleuroglyphus ovatus* (Figs. 44 and 45) bear a striking resemblance to those of *Acarus siro*. With the exception of the outer humeral all the metapodosomatic setae are short, scarcely more than bristles. The lumbar members of the group are slightly larger than the humerals and very stiff. In the female all the metapodosomatic setae are distinctly pectinated. In the male the pectinations are variable, appearing in some individuals, disappearing in others. The third lumbar seta is the only one that appears to be consistently pectinated.

As above, *E. pedispinifer* (Figs. 46 and 47) introduces a chaetotactic pattern that will be followed in the subfamily Rhizoglyphinae. The outer humeral seta is the only member of the humeral group that attains any length. The other three setae are seldom much more than bristles. In the lumbar group the third is the longest, but even when it reaches its maximum length as in the female (*vide* Fig. 47), it is scarcely three times as long as either of the other two.

In pattern and disposition, the humeral setae of *C. spininarsus* (Figs. 48 and 49) are very similar to those of *E. pedispinifer*. The lumbar setae, however, show some evidence of the penchant that this genus has for dimorphic males. The first two setae of this group are almost identical in the two sexes. The third seta is about twice as long in the male as it is in the female. In those species that have heteromorphic males, this tendency is carried even further with the result that almost all the body hairs are much longer than those of the females or homomorphic males.

The chaetotactic pattern of the humeral and lumbar setae of *R. rotundatus* (Figs. 50 and 51) is so similar to that of *C. spininarsus* that there is little need to discuss it further, except to state that, owing to the shortening of the body and the acquiring of the globular shape, the first lumbar seta (5) appears to have moved forward and taken up a position in the humeral group.

R. echinopus (Figs. 52 and 53) follows the same general pattern, though here the setae of the humeral group are longer and the first lumbar seta is closer to its normal position than in the preceding species.

In *H. carpio* (Figs. 54 and 55) the setae of the metapodosomatic group have been so reduced in number that only the "fixed" outer humeral seta (4b) and the third lumbar seta (7) remain. No setae pits or markings can be found to indicate where the other setae might have been.

Setae of the Opisthosoma

The opisthosoma bears seven pairs of major setae, which, for the most part, arise from positions close to the posterior margin of the body. With the exception of the two postanal setae (the anterior 11, and the posterior 13), which have considerable taxonomic value and are capable of some migration, none of them has moved far from its primitive position. In examining these setae the greatest variation that may be noted is not in their disposition, though there is some slight change of pattern, but in their nature: i.e., the body setae of the subfamily Acarinae are very slender, flexible hairs, whilst in the Rhizoglyphinae they are shorter, stiffer, and whip-like.

In *T. infestans* (Figs. 40 and 41) the majority of the opisthosomatic setae arise from positions close to the margin of the body and are fully as long as the entire animal. Structurally, each seta is a simple shaft without any special type of base or socket (the setae in caloglyphid mites have bulbous bases), and with such a gentle and imperceptible taper from the base to the tip that its sides appear to be parallel. In the male the posterior postanal seta (13) arises immediately behind the anterior (11) and both are placed posterad of the anal copulatory suckers in such a manner that all three form a parallel line with the mid-line of the body. The former (13) is quite long and slender; the latter (11) is nothing more than a mere bristle. In the female, the same arrangement is found except that the anterior postanal seta (11) is slightly longer. All the setae except the last mentioned are definitely pectinated.

As may be seen from the drawing, the setae of *A. siro* (Figs. 42 and 43) are relatively much shorter and heavier than those of the preceding species. Only two of these setae ever attain any length, namely, the ventral submarginal (12) and the marginal (14), both of which are slightly shorter than the width of the body in the male and almost equal to one-half the width of the body in the female. Compared with the chaetotactic pattern of *T. infestans*, that of *Acarus siro* shows some modifications. In the male, the anterior postanal seta (11) has been displaced laterally to take up a position between the middle (10) and ventral (12) submarginals. The posterior postanal seta (13), however, remains in relatively the same position. In the female, the former of these (11) is placed opposite the gap between the second and third anal setae, whilst the latter (13) is on a level with the last.

The opisthosomatic setae of *Aleuroglyphus ovatus* (Figs. 44 and 45) are reminiscent of those of the males of *Acarus siro* in that only two, the ventral submarginal (12), and the marginal (14), ever attain any length. These are almost as long as the body is wide in the females and slightly shorter in the males. The outer (8) and inner (9) submarginal setae are quite short and

stiff in both sexes. In some rather rare females the former of these is so heavily pectinated near the tip that it appears to be tufted. Converging towards the mid-line and advancing slightly from the position found in *A. siro*, the anterior (11) and posterior (13) postanal setae of the male form a concave line behind the anal copulatory suckers. As far as these last mentioned setae are concerned, the female has abandoned the chaetotactic pattern of *A. siro* and returned to an arrangement similar to that found in *T. infestans*.

The setae of *E. pedispinifer* (Figs. 46 and 47) are relatively short (never attaining a length equal to one-half of the width of the body), whip-like, and bulbous-based, three characters that show the caloglyphid affinities of this genus. The postanal setae (11 and 13) of the male are placed in a crescent-shaped line similar to that found in *Aleuroglyphus ovalus*, though in this species the anterior seta (11) arises from a position slightly anterad of that of the latter. In the female they have adopted a chaetotactic pattern very similar to that of *Acarus siro* in that the anterior seta (11) is opposite the space between the second and third anal setae and the posterior (13) is on a level with the fourth. Unlike the condition found in *A. siro* and indicative of the trend that is common throughout the Rhizoglyphinae, the postanal setae of the female are reduced to little bristles scarcely longer than any of the anal setae.

C. spinitarsus (Figs. 48 and 49) exhibits a chaetotactic pattern fundamentally similar to that of *E. pedispinifer*. As a characteristic of the sexual dimorphism that is common to most species of the genus *Caloglyphus*, the setae of the male are a half longer and slightly heavier than those of the female. In those species that have heteromorphic males, the tendency to long setae is even more pronounced, with the result that some of the opisthosomatic setae are two-thirds as long as the body. The anterior (11) and posterior (13) postanal setae of the male are placed immediately posterad of the anal copulatory sucker and equidistant from each other and the latter structure. In the female these setae arise from positions close to the anal setae (*vide* Fig. 49).

In *R. rotundatus* (Figs. 50 and 51) the setae retain the same position, though as a result of the rotundity of the body they appear to be farther apart. It should also be noted that, even though they are thinner and longer, they still retain their bulbous bases. Reminiscent of *Aleuroglyphus ovalus*, the anterior (11) and the posterior (13) postanal setae of the male, form a flattish arc behind the anal copulatory suckers. In the female these setae are placed beside the anal setae.

The dorsal chaetotactic pattern of the opisthosoma of *R. echinopus* (Figs. 52 and 53) is very similar to that of *R. rotundatus*. The ventral pattern, however, shows some modifications that, in the female, are occasioned by the migration of the anus to a terminal position. Strangely enough, the arrangement of the ventral setae in both sexes is like that of *T. infestans*. In the male, the anterior postanal seta (11) arises immediately posterad and slightly laterad of the anal copulatory sucker; the posterior postanal

seta is placed just behind it (13) and, with the ventral submarginal seta (12), forms a transverse line across the back part of the body. True, this line is more distinct in *R. echinopus* than in *T. infestans*, but the reason for this is that the setae are relatively longer and closer together. The likeness is even more striking in the female where the two postanal setae (11 and 13) are placed respectively before and after the last anal seta. The ventral submarginal seta (12) has migrated anteriorly and mesially to occupy a position beside the fourth anal seta.

The opisthosoma of *H. carpio* (Figs. 54 and 55) assumes a decidedly different form in the two sexes. In the female it retains the globose shape typical of acarid mites, whereas in the male the terminal end is modified into an odd looking fan-like structure composed of four chitinous lobes terminated by a fringe of cilia. Accompanying these more fundamental changes, the setae have undergone some modification. Some, such as the middle submarginal (10), have disappeared entirely from both sexes; others, such as the marginal (14) and posterior postanal setae (13), appear to have lost their identity only in the male by being included in the "telson." The two lobes of the telson are thought to be homologous, in part at least, with the missing setae because their terminal fringe is composed of actinochitin (a substance found in setae and their derivatives). In the female the anterior (11) and posterior (13) postanal setae are located beside the anus and seem to have taken the place of the last three anal setae. It is possible, of course, that these setae have disappeared entirely and only the anal setae remain.

Morphological Comparison and Relationship of the Various Genera

Certain tentative conclusions may be drawn from the comparative morphological studies presented above. (i) The family Acaridae, as understood in this paper, is a well integrated natural unit. (ii) The origin and development of certain variable characters proceeds in a consistent manner. (iii) By using these characters (i.e. the tarsal and body setae) the species may be arranged in a sequence with *Tyrophagus putrescentiae* at the one end and *Rhizoglyphus echinopus* at the other. Once such a series is established the question arises as to which is the beginning and which the end. To determine this, it is necessary to examine the immature stages (larvae and nymphs) of the species concerned because the nymphs retain structures that their adults have lost or at least modified, but that are common to the adults of other species. In this connection, Oudemans has advanced an hypothesis, which is really nothing more than a modification of the recapitulation theory, that, when the nymphs and immature stages of one species resemble the adults of another, it indicates that the first species is phylogenetically younger than the second. As an example of the point in question we might note that certain of the body setae of the nymphs of *Tyrolichus siculus* are similar to those of the adults of *Tyrophagus putrescentiae*, whereas these same setae in the adult of

Tyrolichus siculus assume a different form*. The application of Oudemans' hypothesis (35) would indicate that *Tyrophagus putrescentiae* is, phylogenetically, the older species and that the evolutionary trend is from this species to *Tyrolichus siculus*. It should be noted that the latter was not included in the above-mentioned series for sake of brevity but that it occupies a taxonomic position between *Tyrophagus putrescentiae* and *Acarus siro*. Several other similar examples could be cited from the species studied that would substantiate this argument and indicate that this is the true direction of development. Thus it would seem that we are justified in assuming that *T. putrescentiae*, occupying as it does the one end of the sequence, stands at the beginning of the series and closest to the prototype of the family.

Genus Tyrophagus.** As the representatives of this genus and their taxonomic position have been discussed elsewhere in the paper, there is no need to mention them here except to say that this appears to be the most primitive genus in the family (i.e., the oldest and closest to the ancestral prototype).

Genus Tyroborus.—This is a genus of very doubtful position and authenticity. Its single species, *Tyroborus lini* Oudms., was described by Oudemans in 1924 from a single male that he found in some old linseed meal. It is similar to *Tyrophagus putrescentiae* in all major respects such as the length of the principal hairs, but differs from it in having the second dorsal terminal seta reduced to a small spine. In this latter respect it is similar to *Tyrolichus casei*. From the various descriptions available, it would seem that the systematic position of the genus *Tyroborus* would be more clearly expressed if it were reduced to a subgenus in the genus *Tyrophagus* [but of more recent origin than the subgenus *Tyrophagus (sensu stricto)*].

Genus Tyrolichus.—So closely does this genus resemble the genus *Tyrophagus* that one is tempted to regard it as a subgenus of the latter.*** There are, however, a few characters that separate it quite nicely and others that show that an affinity exists between it and the genus *Acarus*. Its relationship with the genus *Tyrophagus* is most clearly shown in the general facies and build of the body, shape of the legs, and lack of sexual dimorphism. Taking *Tyrolichus siculus* (F. & R.) (one of its two species, the other being *T. casei* Oudms.) as an example, we note that it differs from any of the members of the genus *Tyrophagus* in the following characters: the equal length of the four propodosomatic setae; the reduced length of, and lack of pectination on, the posterior opisthosomatic setae; the possession of a "parasub-basal" seta (*vide infra*); and the modification of the second dorsal terminal seta (7) into a small spine. Displaying atavistic tendencies, the nymphs of *Tyrolichus siculus* differ from their adults and resemble those of *Tyrophagus putrescentiae* in the

* For a description of the differences, see p. 168.

** For a schematic arrangement of the genera in their tribes and subfamilies, see Fig. 3.

*** Ewing and Nesbitt (10) reduced this to a subgenus in the genus *Tyrophagus*. In the light of the evidence presented above, I think that its position would be better expressed by giving it generic rank.

retention of certain tyrophagid characters, viz., longer inner propodosomatic setae, short and stiff first and second lumbar setae, and very long posterior opisthosomatic setae.

Tyrolichus siculus and *T. casei* show their affinities with the genus *Acarus* in the equal length of the four propodosomatic setae, the plump heavily pectinated pseudostigmatic organ, and the possession of a "parasub-basal" seta (3) on the tarsus. The position of the last mentioned seta on the lateral face of the tarsus, intermediate between the origin of the postdorsal median seta (3) of *Tyrophagus putrescentiae* and the parasub-basal seta of *A. siro*, lends additional weight to the argument that the parasub-basal seta is homologous with the postdorsal median seta. In other words, it is as if we could see this seta in the process of migration from the dorsal to the lateral position. Since it is not in its true position, the word "parasub-basal" was placed in quotation marks to indicate this. The genus *Tyrolichus* also shows affinities with the kindred genus *Aleuroglyphus* in the possession of a small spine in place of a second dorsal terminal seta (7). From this brief review of the data it is obvious that the genus *Tyrolichus* bears a close relationship to the genus *Tyrophagus* of the tribe Tyrophagini and that it has affinities with both the genera *Acarus* and *Aleuroglyphus* of the tribe Acaridini.

Genus Acarus (Tyroglyphus).—In any series such as the one we are studying, there are units that appear to be more stable and exhibit greater individuality than others. Such a group is the genus *Acarus*, which, whilst retaining certain features in common with the previous species and displaying others that foreshadow characters found in subsequent examples, maintains its own discrete entity. Examining each of these categories in turn with *A. siro* as the representative of the genus, we may first note those features that are common to more primitive types. The most important of these are: the equal length of the propodosomatic setae; pectinations on such setae as the rostral, propodosomatic, outer humeral (rarely), and certain tarsal setae such as the ventral distal seta of the tibia; retention of the setiform shape of the second dorsal terminal seta of the tarsus (7); and the type of hypopus. In the second place, *A. siro* adumbrates features of subsequent species by exhibiting such caloglyphid characters as: the length and general whip-like nature of the body setae (note that the middle humeral seta is no longer of equal length to the outer but reduced to a small bristle); the position of the parasub-basal seta; the slightly increased size of the tarsal setae; the more dorsal position of the cervical bristle (*vide* pp. 150 and 161)*; and the arrangement of the anterior (11) and posterior (13) postanal setae in relation to the anal setae. Lastly, despite such affinities, the genus demonstrates its individuality, but only in

* In the tribe Caloglyphini this bristle is located near the middle of the lateral edge of the propodosomatic escutcheon; in the Tyrophagini it arises from the lateral face or marginal border of the propodosoma. In *A. siro* it is intermediate in position, being just on the dorsal face and anterior to the first coxa.

the male sex, by the possession of a type of dimorphic male* that is peculiar to this group; the round as opposed to the modified crescent-shaped anal copulatory suckers; and the arrangement of the postanal setae.** Thus in conclusion it may be noted that the genus *Acarus* of the tribe Acaridini is a discrete entity bearing traces of a relationship with the tribe Tyrophagini and showing affinities with the tribe Caloglyphini. In view, however, of the peculiar type of male dimorphism that it displays, it is believed that it is somewhat off the direct line of descent.

Genus Aleuroglyphus.—The genus *Aleuroglyphus* is a group that was created in 1942 by A. A. Zakhvatkin to make a place for the anomalous species *Tyroglyphus ovatus* Troup. From the point of view of comparative studies, it is a most interesting form because it combines structures that are characteristic of both its predecessors and its successors. Undoubtedly, its closest relationship is with the genus *Acarus* of the tribe Acaridini. The general appearance of its body and the shape of the tarsi, the size of the ventral terminal tarsal spines, the nature of Grandjean's organ (*vide* p. 151), and the position of the female anus, lend support to this point of view. The structure of the tarsi (i.e., the position of the parasub-basal seta, the relatively distal point of origin of the mesial and lateral median setae, and the reduction of the second dorsal terminal seta to a spine), the length of the inner propodosomatic setae, and the transverse linear arrangement of the postanal setae of the male, indicate that this genus should be placed between the genera *Acarus* and *Eberhardia*. However, the retention of pectination on the second lumbar seta of the male as well as on all the metapodosomatic setae of the female and the arrangement of the postanal setae (11 and 13) of the latter, place this genus off the direct line of descent by showing that it still retains tyrophagid affinities that were abandoned by *A. siro*.

Genus Eberhardia.—As was pointed out above (*vide* p. 161) the genus *Eberhardia*, coming as it does at the first of the subfamily Rhizoglyphinae,***

* The type of sexual dimorphism exhibited by *Acarus siro* is altogether different from that found in any other Acarid. In the subfamily Rhizoglyphinae, where such manifestations are frequently encountered, the heteromorphic males are always in the minority (only about 10% of the male population) and the modification chiefly affects the third leg (*vide* p. 158). In *A. siro*, however, all the males are heteromorphic and it is the first leg that is modified by the possession of a large spine on the femur. The whole subject of the production or cause of heteromorphic males in the Rhizoglyphinae is very interesting and complex. Were they not in the minority, their presence could be explained by saying that they are the true males and that the homomorphic males were intersexes. If they are caused by hereditary factors, the inheritance must be quite complex because I have bred heteromorphic males to their siblings for several generations (6) and have not obtained any increase in the percentage of such males. It is doubtful if their production is due to complex environmental factors though that is possible. In time it probably will prove to be a genetical problem as Foa (11, 12) has suggested.

** In the series studied, the arrangement of the male postanal setae follows three patterns. (i) In the tribe Tyrophagini and genus *Caloglyphus* the posterior (13) setae are placed behind the anterior (11) (*vide* Figs. 40 and 48). (ii) In the genus *Acarus* they arise from the margin of the opisthosoma (*vide* Fig. 42). (iii) In all the remaining examples they are placed side by side forming a transverse concave line behind the anal copulatory suckers (*vide* Figs. 44, 50, and 52).

*** It should be noted that the subfamily Rhizoglyphinae, as exemplified by such genera as *Eberhardia*, *Caloglyphus*, *Rhizoglyphus*, and possibly *Schwiebia*, is a much more compact group than the subfamily Acarinae and that as a consequence, the differences from group to group are not as great as in the latter and the genera do not appear as such distinct units.

initiates changes (such as the modified nature of the nuchal seta and the changed position of the cervical bristle) that are characteristic of the whole subfamily. Unfortunately for accuracy of description and nicety of taxonomic position, it has little individuality of its own; and on general examination, most, if not all, of its species appear to be nothing more than little Caloglyphids. They do exhibit, however, certain minor differences that have been retained from more primitive species and that are sufficient to set the genus apart as a separate, even though not essentially a distinct, group. Some of these are: the moderately heavy pectination on the pseudostigmatic organ; the arrangement of the postanal setae in both sexes; the position of the female anus* (almost intermediate between that of *A. ovatus* and that of *C. spinitarsus*); and the nature of the tarsal setae (especially those on tarsus I).

Whilst not a large genus it may be divided quite readily into two subgenera, *Eberhardia* (*sensu stricto*) and *Cosmoglyphus* Oudms., on the presence or absence of sexual dimorphism and the types of hypopi produced.** The latter subgenus will be discussed first because it appears to be on the direct line of descent leading to the genus *Caloglyphus*. Taking *E. (Cosmoglyphus) pedispinifer* as a typical example of the group, we may note that its tarsi are intermediate in position between those of *A. ovatus* and *C. spinitarsus*. On tarsus I the mesial and lateral median and mesial terminal setae retain their primitive position and setiform nature; the dorsal median seta has migrated proximally and begun to adopt a shape similar to its homologue in the genus *Caloglyphus*; the second dorsal terminal seta has become a definite spine, which shape it will retain, though considerably enlarged, throughout the remainder of the series; and both macrosense and microsense setae arise from the same membranous cushion.

The subgenus *Eberhardia* is a little more difficult to place exactly. If only its adults were used as the basis for comparison, it could be assigned to a position between its sister subgenus and the genus *Caloglyphus*. The adults of *E. michaeli* Oudms., for example, show affinities with both groups; in the general shape of the body and nature of the tarsal setae, they resemble *E. (C.) pedispinifer****; in the possession of sexual dimorphism and heteromorphic males they undoubtedly exhibit strong leanings towards the genus *Caloglyphus*. The chief difficulty concerns the hypopi. Unlike those of either the subgenus *Cosmoglyphus* or the genus *Caloglyphus*, which possess well sclerotized ventral sucker plates, the hypopi of this subgenus have weakly sclerotized plates and poorly developed and widely separated suckers. Despite the above mentioned

* In a kindred species, *E. (C.) krameri* Oudms., the anus is still more anteriorly placed, almost up to the position found in *C. berlesei*.

** In the subgenus *Cosmoglyphus*, sexual dimorphism is almost absent and heteromorphic males are never encountered. In the subgenus *Eberhardia* just the reverse of this is true. In the hypopi of the former, the abdominal sucker plate is well formed; in those of the latter, the suckers are smaller and farther apart and there is little evidence of a well chitinized plate.

*** There is one slight difference that might be mentioned. In *E. michaeli* the mesial terminal seta is reduced to a spine similar to that found in *C. spinitarsus*.

adult characters, such hypopi would place this group off the direct line of descent. If, however, a second type of hypopus could be found with well developed sucker plates, this group would make a most interesting link because it would be the first in which true heteromorphic males would have been found. The possibility of such hypopi existing is not too remote when we consider that *A. siro* has two such types of hypopi (one with well sclerotized and one with poorly sclerotized sucker plates) and that the subgenus *Eberhardia* is not a well known group.

Genus Caloglyphus.—In examining the subfamily Rhizoglyphinae as a whole, certain conclusions are patent. One of these is that it is a much more highly integrated group than its sister subfamily Acarinae. As a result of this and the more gradual evolution of its characters, none of the subgroups may be defined with extreme accuracy (*vide* p. 177). This is true of the subgenera *Cosmoglyphus* and *Eberhardia*, and the genus *Caloglyphus*, which appear to be intergrading groups. The last of these continues the trends that are initiated in the first and carries them to their logical conclusion, with the result that it stands close to the culmination of the series. For example, the tarsal chaetotactic pattern is completed. In *C. spinitarsus*, *longitarsus*, and *berlesei*, to take but three samples from a large genus, the mesian and lateral median setae of tarsus I have migrated to the distal end of the segment and developed falcate ends; the mesial terminal seta (8) has become spine-like; the second dorsal terminal seta (7) has metamorphosed into a thorn-like process of the tarsus; and the caruncular seta (6) has adopted a characteristic shape. Similar changes have taken place on the other legs; and the copulatory suckers on the fourth tarsus of the male have assumed the distal position. Furthermore, the general body structure shows little change from that of the previous genus. Contingent upon the greatly increased size of the female opisthosoma, the anus appears to have migrated anteriorly until it is close to the centre of the body.

Undoubtedly the genus *Caloglyphus* originated from an eberhardian form, if this subgenus is admitted to the direct line of descent (*vide supra*) or, if not, from a proteberhardian type that introduced sexual dimorphism. It finds its closest relationship with the two subgenera (*Eberhardia* and *Cosmoglyphus*) of the genus *Eberhardia*. On the other hand, strong affinities exist between it and the genus *Rhizoglyphus*. Despite, however, the great similarity that includes the manifestations of sexual dimorphism and the types of hypopi produced, there are differences that indicate that these two genera are not lineally related but occupy comparable positions on the arms of a dichotomous branching.

Genus Rhizoglyphus.—Occupying a comparable position, the genus *Rhizoglyphus* differs from its related genus *Caloglyphus* in one major respect. As was noted above, the latter is one of those remarkable taxonomic groups that seem to have arrived at its destination without any inconsistencies. The genus *Rhizoglyphus*, on the contrary, is not uniform. It retains such primitive characters as the setiform nature of the mesial terminal tarsal seta (8), the

terminal position of the female anus, and the transverse arrangement of the male postanal setae. In addition to these it exhibits complex structures that are peculiar to this genus; viz., the generally heavy build of the body, which is particularly noticeable in the strongly sclerotized areas about the articulation of the anterior coxae; the massive heavily-spined legs, which, terminating in short conical-shaped tarsi with large claws, lack a caruncle; the size and position of the dorsal median seta (3)*; the lack of a parasub-basal seta; the crescent-shaped falcations on the terminal tarsal setae; and the reduction of the terminal tibial seta on the fourth tarsus of the male to a small spine (*vide* Figs. 24 and 26). Bridging the gap or intermediate between these two related, but distinct genera, is to be found the interesting little form, *R. rotundatus*, which was discovered on rotting mushrooms. To an otherwise normal member of the genus *Rhizoglyphus* it has added such caloglyphid features as a conical-shaped parasub-basal seta on tarsus I; the central position of the female anus; the relatively longer tarsi; and the possession of a seta instead of a spine on the fourth tibia of the males.

To explain the retention of the aforementioned primitive characters and to account for the more peculiar ones, it is necessary to postulate that the genus *Rhizoglyphus* arose from the caloglyphid stalk somewhere in the vicinity of the proteberhardian ancestral type** and developed along its present lines. Compared with the free-living agile Tyrophagids, these ponderous slow-moving mites appear to be degenerate forms. There is some ground, although in the present state of our knowledge the argument is very tenuous, for accepting this thesis and considering the genus *Rhizoglyphus* the most degenerate group in the family. (i) In food requirements and habitat preference, its members can live only on exceedingly damp***, putrefying fungus or organic material whereas some of the closely related Caloglyphids can live on farinaceous materials. (ii) In many anatomical respects, such as the shape of the body and nature of the tarsi, *R. echinopus* resembles a species of the genus *Sarcoptes*, one of the degenerate parasitic mites of the superfamily Sarcoptiformes.

Genus Schwiebea.—The genus *Schwiebea* is another genus of very doubtful authenticity. In writing of *S. talpa*, Vitzthum (47) states that it differs from *R. echinopus* only in the possession of an opisthosomatic shield. In the course of his description he comments on the fact that many previous authors may have overlooked this structure, as it is very difficult to see, and that as a consequence *S. talpa* may be a synonym of the "*R. echinopus*" of some earlier worker. Should the genus be allowed to stand, however, it would occupy a position very close to the genus *Rhizoglyphus*.

* Immediately in front of the microsense seta (*vide* p. 156).

** This ancestral form must have had heteromorphic males; the mesial and lateral setae of the tarsi in the terminal position and the mesial terminal seta of setiform shape; the postanal setae of the male in a transverse row; and the female anus in a relatively terminal position.

*** In fact the members of this genus are the only ones in the family that can live continuously in water (or a material like vegetable broth) that almost covers them.

Genus Thyreophagus (Monieziella).—All the species that have been examined so far in this paper have maintained a common chaetotactic pattern with the result that they formed a neat systematic unit. There remains, however, a small group of species belonging to the two closely interrelated genera *Thyreophagus* and *Histiogaster*, which differs from the aforementioned in exhibiting a simplified pattern of dorsal setae and in possessing males with modified opisthosomata. These two genera are so similar that unquestionably they arose from a common ancestor; and the likeness that they bear to the genus *Rhizoglyphus* would indicate that they separated from the rhizoglyphid stalk at a comparatively early date but after the loss of the parasub-basal seta by the latter. The characters that serve to separate them are of a minor nature and concern relative proportions rather than any fundamental differences. Thus a study of the length of the tarsi, the number of dorsal setae, and the type of male opisthosoma, indicates that the genus *Thyreophagus* is simpler than *Histiogaster* and undoubtedly closer to the ancestral prototype. In *T. entomophagus* (Lab.), for example, the arrangement of the tarsal setae, and the shape of the legs, indicate a close relationship with such highly specialized types as *R. echinopus*, whilst the retention of the setiform shape by these setae demonstrates affinities with more primitive species. On the other hand the chaetotactic pattern* of the dorsal setae and the terminal plate on the male opisthosoma show that this genus has developed a considerable degree of specialization. In such species as *Thyreophagus entomophagus* and *T. angusta* (Banks), the male opisthosoma is terminated by a single chitinous plate that is confluent with the ventral surface of the body.

Genus Histiogaster.—Whilst exhibiting closer tarsal affinities with the rhizoglyphid stock than were noted in the previous group**, the genus *Histiogaster* seems to have progressed further in developing its own individuality. For example, there has been a greater reduction in the number of dorsal setae and an enlargement of the terminal opisthosomatic plate into a fan-like structure. In *H. carpio* the pseudostigmatic organ is reduced to a tiny peg; also the postanal (13) and marginal (14) setae appear to be wanting in the male. The expression "appear to be wanting" is used advisedly because, as was noted above (*vide p. 166*), the four terminal lobes of the tail-piece may be homologous with the missing setae***. As a result of the above mentioned modifications, the genus *Histiogaster* appears to be more complex than *Thyreophagus*. Moreover, when the tarsi are compared it is obvious that the former

* A considerable amount of simplification has taken place in the number of setae found. On both of the species mentioned above, the following setae are missing: the inner propodosomatic (3a), the inner (4c) and middle (4a) humeral, the first (5), second (6), and third (7) lumbar, and the middle submarginal (10) setae. In the female the anterior postanal seta (11) is also wanting.

** *Genus Thyreophagus*—*vide supra*.

*** An examination of Fig. 54 will show that in *H. carpio* there is a ventral chitinous plate that is confluent with the ventral face of the opisthosoma as in *T. entomophagus*, and that the terminal lobes, the homologues of the setae, are attached to it.

bears a closer relationship to *R. echinopus* than the latter. It is true that the tarsi of *T. entomophagus* bear a superficial resemblance in size and shape to those of *R. echinopus*, but when we consider the relative position, shape, and size of these setae, the balance is in favour of *H. carpio*. It should be added in conclusion that the terminal setae in both groups never bear falcate ends and that the mesial terminal seta in *H. carpio* has the spine-like shape of caloglyphid mites.

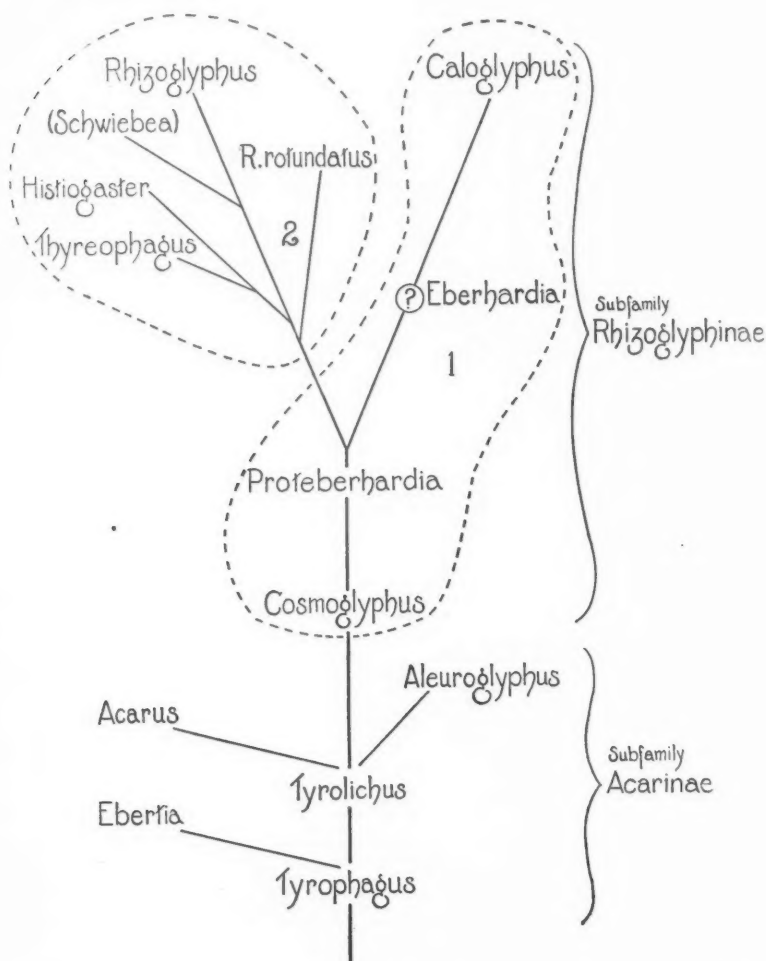


FIG. 3. A schematic representation of the relationships in the family Acaridae. (Vide: "Morphological comparison and relationship of the various genera" for a discussion of the characteristics used in preparing this chart.) 1. Tribe Caloglyphini. 2. Tribe Rhizoglyphini.

A Synopsis of the Tribes and Genera of the Family Acaridae

Family ACARIDAE (TYROGLYPHIDAE)

Body distinctly divided by a transverse groove into a proterosoma and hysterosoma. Body stout, white or fawn; integument usually smooth and shiny, rarely rough. Chelicerae chelate. Propodosoma bears five pairs of setae (i) rostral setae (ii) Grandjean's organ in Acarinae = nuchal setae in Rhizoglyphinae (iii) cervical bristles (iv) outer propodosomatic setae and (v) inner propodosomatic setae (a reduction in the number of these setae is to be found in the genera *Thyreophagus* and *Histiogaster*). Anterior part of propodosoma usually covered by a shield. Pseudostigmatic organ present in all genera. The general chaetotactic pattern is shown in Fig. 1. Male and female genital opening is between coxae III and IV. Two distinct copulatory suckers are located on either side of the male anus. Epimera I united to sternum, all others free. All coxae but IV bear a spine on the ventral surface. Tarsi may be longer than tibia + genu; tarsus I bears (i) macrosense seta with a microsense seta before it at its base; (ii) sub-basal seta with the occasional addition of a parasub-basal seta; (iii) a group of four median setae; (iv) a ventral terminal group of three to five spines; (v) a dorsal terminal group of four long setae that may be modified; (vi) a claw surrounded by a caruncle that is never pedunculate. Tarsus II bears a macrosense seta but neither a microsense seta nor a parasub-basal seta. Tarsus III in heteromorphic males is modified as a large claw. Tarsus IV in the female bears two lateral spines; in the male these are replaced by two suckers except in the genus *Thyreophagus* where there is only one. In the more primitive members of the group the tarsal setae are thin, slight hairs, in the more advanced members they become modified as large spines. Larvae have a well developed cylindrical or pin-shaped "Bruststiele" (urstigmata).

Subfamily ACARINAE

A. 1. Forms of medium size (0.40 — 0.75 mm.) males and females are strictly homeomorphic with the exception of the genus *Acarus* where the males bear a large spine on the femur of leg I. Grandjean's organ a thin root-like structure adhering closely to the lateral wall of the body. Cervical bristles usually large, often showing pectinations, located either marginally or dorsally on the anterior part of the propodosoma before, or on a level with, the first trochanters. Inner propodosomatic setae may be either equal to or longer than the outer [Oudemans says that they are shorter in the genus *Ebertia* (vide infra)]. Anal copulatory papillae in all forms except *Acarus* are of Oudemans' first type. Legs slender, tarsi usually equal in length to, if not longer than, the combined length of genu + tibia. Tarsal setae flexible, more or less hair-like. Lateral and mesial median setae unmodified and in middle of tarsus. Macrosense and microsense setae do not arise from the same membranous cushion. Caruncle well developed. Anal cleft in the female close to the posterior edge of the opisthosoma. B.

Tribe TYROPHAGINI

B. 1. No parasub-basal setae present on tarsus I; postdorsal median and dorsal median setae, however, are present. Ventrodistally the tarsi bear three to five little spines; terminal setae long, hair-like, and unmodified. The only exception is the second dorsal terminal seta, which may be reduced to a small spine. Males strongly homeomorphic, i.e., leg I shows no modifications (may be slightly heavier than that of the female). Most of the longer body setae are pectinated. The genera of this tribe may be separated as follows:

- C. 1. Skin granulated; cervical setae short and smooth; tarsi dorsodistally without spines; propodosoma with a transverse row of four setae, the inner pair of which are shorter than the outer. Genus *Ebertia* Oudms. 1924 (33).

Haplotype: *Tyroglyphus australis* Oudms. 1917 (28).*

- C. 2. Skin polished; cervical setae long and distinctly pectinated (like feathers); dorso-distal spines of tarsi, when present, minute; propodosoma with transverse row of four almost equally long setae. D.

- D. 1. Propodosoma with a transverse row of four almost equally long setae; hysterosoma with only one pair of short bristles (No. 4c); second lumbar seta (No. 6) almost equal in length to the posterior setae; tip of tarsus with one small dorsal spine, three to five small ventral spines. Genus *Tyrolichus* Oudms. 1924 (31).

Orthotype: *Tyrolichus casei* Oudms. 1910 (26).

* From Oudemans' descriptions there is considerable doubt in my mind concerning the identity of this species. From the above notes one would be inclined to associate it with the genus *Aleuroglyphus* in the tribe *Acaridini*, but I cannot be certain of this until I have seen a specimen to examine the disposition of the tarsal setae and especially the position of the parasub-basal seta.

- D. 2. Propodosoma with a transverse row of four setae, the inner pair of which are longer than the outer; hysterosoma with two pairs of short bristles (Nos. 4c and 6); the first lumbar setae (5) may be short or of intermediate length.....Genus *Tyrophagus* Oudms. 1924 (31)...E.
- E. 1. Tarsi dorsodistally with one spine (= second dorsal terminal seta No. 7). Ventrodistally with three to five spines.....Subgen. *Tyroborus* Oudms. 1924 (33).
Haplotype: *Tyroborus lini* Oudms. 1924 (34).
- Tarsi dorsodistally without a spine, ventrodistally with three to five spines....F.
- F. 1. Claw and caruncle normal; maxillary plate normally cleft; in adults setae on coxae III and IV short.....Subgen. *Tyrophagus* Oudms. 1924 (31).
Orthotype: *Acarus putrescentiae* Schr. 1781 (42).
- F. 2. Claws short; caruncle minute; maxillary plate deeply cleft; almost until base of palps; in adults hairs on coxae III and IV long.....Subgen. *Povelsenia* Oudms. 1924 (33).
Haplotype: *Tyroglyphus neotropicus* Oudms. 1917 (28).

Tribe ACARIDINI

B. 2. Parasub-basal seta present on tarsus I; postdorsal median seta, however, absent. Ventrodistally the tarsi bear three to five little spines, the most ventral ones of which are relatively quite large and conspicuous; dorsal terminal setae long, hair-like, and unmodified (in the genus *Aleuroglyphus* the second dorsal terminal seta (No. 7) has been reduced to a spine). Males of the genus *Acarus* are strongly heteromorphic, i.e., have a large process on the femur of leg I. Few of the body setae show pectinations. The genera of this tribe may be separated as follows.....C.

- C. 1. Leg I of male spindle-shaped, much heavier than that of the female, and characterized by a large spinous process on the femur; ventrodistally the tarsi in both sexes bear one large spine and two to four smaller ones (*vide* p. 157); many of the dorsal setae (e.g. 4a and c, 5, 6, and 7) quite short; the propodosomatic and humeral setae are frequently pectinated.....
Genus *Acarus* Linn. 1758; (*Tyroglyphus* Latr. 1796 (21)).
Logotype: *Acarus siro* Linn. 1758 (22).
- C. 2. Leg I of the male scarcely larger than that of the female, does not bear a large spine on the femur; ventrodistally the tarsi in both sexes bear three relatively large, conspicuous spines (the inner spine is usually the largest); the second dorsal terminal seta (No. 7) is reduced to a spine. (This is most noticeable on tarsi III of the male and III and IV of the female); many of the dorsal setae are quite short and some bear pectinations.....Genus *Aleuroglyphus* Zakh. 1940 (52).
Orthotype: *Tyroglyphus ovatus* Troup. 1879 (46).

Subfamily RHIZOGLYPHINAE

A. 2. Mainly large forms (0.70 - 2.0 mm.), frequently showing well defined sexual dimorphism which, in the male, consists of longer body setae and the third leg modified as a claw-like structure without an ambulacrum. Nuchal setae (= Grandjean's organ) distinct horn-like processes standing free from the body. Cervical bristles minute, sometimes absent, located toward the middle of the lateral edge of the propodosomatic shield. Inner propodosomatic setae shorter than outer; may even be vestigial. Anal copulatory papillae of males of Oudemans' first type. Legs relatively massive, frequently very short and thick, setae, and tarsal setae in particular, often modified as stout spines. Lateral and mesial median setae distally placed; may have falcate ends. Microsense and macrosense seta located on the same membranous cushion. Caruncle may or may not be present. Anal cleft in the female may be in centre of opisthosoma or slightly removed from hind margin of body.....B.

Tribe CALOGLYPHINI

B. 1. Dorsal median setae on tarsus I of normal size (i.e. no longer than the ventral median seta) well removed distally from the base of the macrosense seta. Sub-basal and parasub-basal setae always present. All legs relatively long (with the exception of leg III in the heteromorphic males); tarsi with somewhat parallel sides, usually longer than the combined length of the two preceding segments (genu + tibia) claws normal, slight caruncle; apical bristle on tibia IV of male a normal seta. Inner propodosomatic setae and cervical bristles

quite small but always present. Never an opisthosomatic shield. Anal copulatory suckers (papillae) not surrounded by a chitinous ring; belong to Oudemans' first type. Female anal slit placed in either the centre or towards the hind margin of the opisthosoma. The genera of this tribe may be separated as follows:.....C.

- C. 1. Pseudostigmatic organ peg-like or setiform, never pectinated. Mesial and lateral median setae of tarsi I and II are terminally placed and have their free ends dilated in shape of a paddle; first dorsal terminal seta and terminal setae of tarsi III and IV bear falcate ends. Copulatory suckers on tarsus IV of the male situated in the distal half of the segment. Sexual dimorphism evident in some species. Species large, 700 μ to 2260 μGenus *Caloglyphus* Berl. 1923 (5).
Orthotype: *Tyroglyphus berlesei* Mich. 1903* (23).
- C. 2. Pseudostigmatic organ usually heavily pectinated (in one or two species the pectinations are sparse). Mesial and lateral median setae on tarsi I and II may or may not be terminally placed; if terminally placed only the mesial median seta bears a small truncate paddle; none of the other terminal tarsal setae on any of the legs are falcate. Copulatory suckers on tarsus IV of the male equidistant between themselves and the ends of the tarsi. Species smaller, 400 μ to 750 μGenus *Eberhardia* (Oudms. 1924) (30)....D.
- D. 1. Mesial and lateral median setae terminally placed; dorsal and ventral median setae spiniform. Sexual dimorphism marked; heteromorphic males frequently encountered. Hypopus without a definite sucker plate, suckers widely separated.....Subgenus *Eberhardia* Oudms. 1924 (30).
Haplotype: *Eberhardia michaeli* Oudms. 1924 (32).
- D. 2. Mesial and lateral median setae either medially or terminally placed; dorsal and ventral median setae setiform. Little evidence of sexual dimorphism. Hypopus with a well developed sucker plate.....Subgenus *Cosmoglyphus* Oudms. 1932 (39).
Orthotype: *Tyroglyphus krameri* Berl. 1881 (4)

Tribe RHIZOGLYPHINI

B. 2. Dorsal median seta on tarsus I a short, stout, conical spine placed immediately before the base of the microsense seta. Sub-basal seta usually present; parasub-basal seta missing except in a few rare instances. All legs relatively short; sides of tarsi taper distally to form a conical-shaped structure; usually quite short, seldom longer than the combined length of the two preceding segments; claws massive, no caruncle, apical bristle on tibia IV of male a short conical spine. Inner propodosomatic setae minute, frequently wanting; cervical bristle not always present. An opisthosomatic shield may be present. Anal copulatory suckers surrounded by a chitinous ring; belong to Oudemans' first type. Female anal slit always close to the hind margin of the opisthosoma. The genera of this tribe may be separated as follows:.....C.

- C. 1. Body chaetotaxy normal, i.e., it follows the typical plan of acarid mites outlined above; opisthosoma may bear a chitinous shield but is normal in shape and similar in the two sexes.....D.
- D. 1. Hind part of propodosoma with a transverse row of four setae of which the inner pairs are minute; terminal setae of the tarsus bear falcate ends; male with suckers on tarsus IV (distal sucker almost on rudimentary caruncle) but without an opisthosomatic shield.....Genus *Rhizoglyphus* Clap. 1869 (9).
Haplotype: *Tyroglyphus echinopus* Fum. et Robin 1868 (13).

* The question of the type for the genus *Caloglyphus* is open to some doubt. Berlese (5) cited *Tyroglyphus mycophagus* as the type in his original description. Prior to this Michael (23) had shown that Berlese's *T. mycophagus* was not the true *mycophagus* of Ménétriér but a new species to which he gave the specific name of "*berlesei*." A comparison of the original descriptions and drawings confirms the English author's position. Accordingly, in the above key, the correct name *T. berlesei* has been substituted. In quoting this name I have condoned Jary's (17) and Zakhvatkin's (51) position but in so doing I realize that they have gone contrary to Opinions 65 and 168 of the International Committee of Zoological Nomenclature. To my mind the correction of a zoological error is preferable to its continuance and an attempt will be made to have an opinion granted on this name.

- D. 2. Hind part of propodosoma with a transverse row of two setae only; terminal setae of tarsus unmodified; male without suckers on tarsus IV but with an opisthosomatic shield.....Genus *Schwiebia* Oudms. 1916 (27).
Haplotype: *Schwiebia talpa* Oudms. 1916 (27).
- C. 2. Body chaetotaxy irregular, i.e., several setae (e.g. Nos. 3a, 4a, and c, 5, 6, and 10) are missing; opisthosoma prolonged into a shelf-like projection on the hind margin of the body of male.....D.
- D. 1. Legs short and stout, tarsal setae setiform; pseudostigmatic organ present; body elongated; terminal plate on male opisthosoma composed of a single lobe—similar to a shelf.....Genus *Thyreophagus* Rond. 1874 (41).
Haplotype: *Tyroglyphus entomophagus* (Lab. 1852 (20)).
- D. 2. Legs longer, tarsal setae inclined to be spiniform; pseudostigmatic organ minute; body globular-shape; terminal plate of male opisthosoma divided, in a fan-like manner, into four distinct lobes.....Genus *Histiogaster* Berlese 1883 (3).
Haplotype: *Tyroglyphus carpio* Kramer 1882 (19).

Acknowledgments

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Note: Figs. 4 to 55 will be found on pp. 182-188.

EXPLANATION OF FIGURES

FIGS. 4-15. *Tarsus I*.

- FIG. 4. *Tyrophagus putrescentiae* (mesial view).
 5. *Tyrophagus infestans* (mesial view).
 6. *Acarus siro* (lateral view).
 7. *Aleuroglyphus ovatus* (lateral view).
 8. *Eberhardia pedispinifer* (lateral view).
 9. *Caloglyphus spinatarsus* (lateral view).
 10. *Caloglyphus longatarsus* (lateral view).
 11. *Rhizoglyphus rotundatus* (lateral view).
 12. *Rhizoglyphus echinopus* (lateral view).
 13. *Schwiebia talpa* (mesial view *Tarsus II*, after Vitzthum).
 14. *Histiogaster carpio* (lateral view).
 15. *Thyreophagus angusta* (mesial view).

Setae: 1, macrosense; 2, microsense; 3, postdorsal median; 4, dorsal median; 5, first dorsal terminal; 6, caruncular; 7, second dorsal terminal; 8, mesial terminal; 9, mesial median; 10, lateral median; 11, ventral median; 12, sub-basal.

Note: seta No. 3 is known as the parasub-basal seta in Figs. 3 to 12.

FIGS. 16-27. *Tarsus IV, male*.

- FIG. 16. *Tyrophagus putrescentiae* (lateral view).
 17. *Tyrophagus infestans* (mesial view).
 18. *Acarus siro* (lateral view).
 19. *Aleuroglyphus ovatus* (lateral view).
 20. *Eberhardia pedispinifer* (lateral view).
 21. *Caloglyphus spinatarsus* (mesial view).
 22. *Caloglyphus longatarsus* (lateral view).
 23. *Rhizoglyphus rotundatus* (lateral view).
 24. *Rhizoglyphus echinopus* (lateral view).
 25. *Histiogaster carpio* (lateral view).
 26. *Caloglyphus armipes*, *Tarsus III*, normal male.
 27. *Caloglyphus armipes*, *Tarsus III*, heteromorphic male.

Setae: a, mesial median; b, ventral median; c, first dorsal terminal; d, mesial terminal; e, second dorsal terminal.

FIGS. 28-39. *Tarsus IV, female*.

- FIG. 28. *Tyrophagus putrescentiae* (mesial view).
 29. *Tyrophagus infestans* (mesial view).
 30. *Acarus siro* (lateral view).
 31. *Aleuroglyphus ovatus* (lateral view).

- FIG. 32. *Eberhardia pedispinifer* (lateral view).
 33. *Caloglyphus spinitarsus* (lateral view).
 34. *Caloglyphus spinitarsus*, tarsus III (lateral view).
 35. *Caloglyphus longitarsus* (lateral view).
 36. *Rhizoglyphus rotundatus* (lateral view).
 37. *Rhizoglyphus echinopus* (lateral view).
 38. *Histiogaster carpio* (lateral view).
 39. *Thyreophagus angusta* (lateral view).

- FIG. 40. *Tyrophagus infestans* (male).
 41. *Tyrophagus infestans* (female).
 42. *Acarus siro* (male).
 43. *Acarus siro* (female).

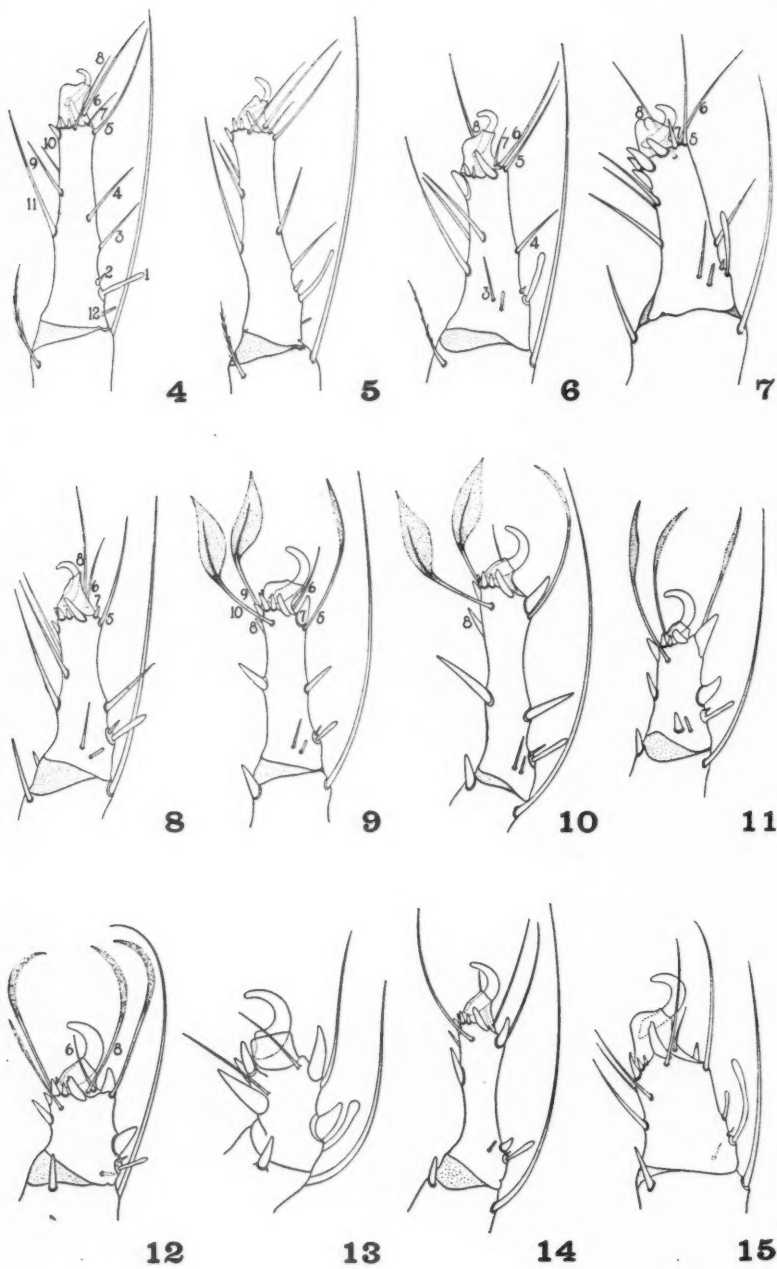
- FIG. 44. *Aleuroglyphus ovatus* (male).
 45. *Aleuroglyphus ovatus* (female).
 46. *Eberhardia pedispinifer* (male).
 47. *Eberhardia pedispinifer* (female).

- FIG. 48. *Caloglyphus spinitarsus* (male).
 49. *Caloglyphus spinitarsus* (female).
 50. *Rhizoglyphus rotundatus* (male).
 51. *Rhizoglyphus rotundatus* (female).

- FIG. 52. *Rhizoglyphus echinopus* (male).
 53. *Rhizoglyphus echinopus* (female).
 54. *Histiogaster carpio* (male).
 55. *Histiogaster carpio* (female).

Note: In Figs. 40-55 (on pp. 185-188), the left side shows the dorsal and the right, the ventral face of the mite. Also the heavy black line below represents 0.1 mm.

Setae: 1a, rostral; 1b, cervical; 2, pseudostigmatic organ; 3a, inner propodosomatic; 3b, outer propodosomatic; 4a, middle humeral; 4b, outer humeral; 4c, inner humeral; 4d, inferior humeral; 5, first lumbar; 6, second lumbar; 7, third lumbar; 8, outer submarginal; 9, inner submarginal; 10, middle submarginal; 11, anterior postanal; 12, ventral submarginal; 13, posterior postanal; 14, ventral submarginal; e, anterior intepimeral; f, anterior paragenital; g, posterior intepimeral; h, middle paragenital; i, posterior paragenital; Δ Grandjean's organ.





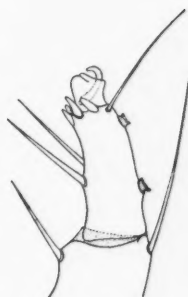
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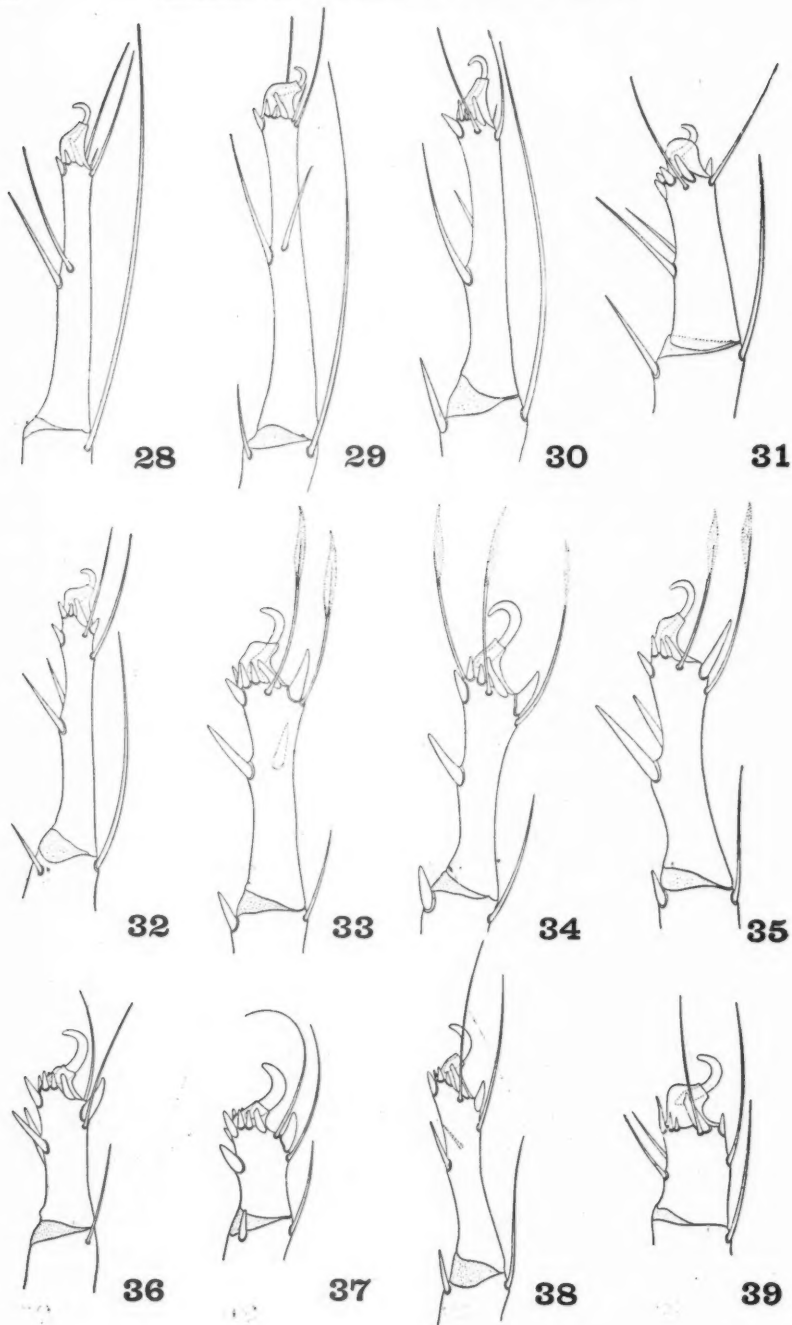
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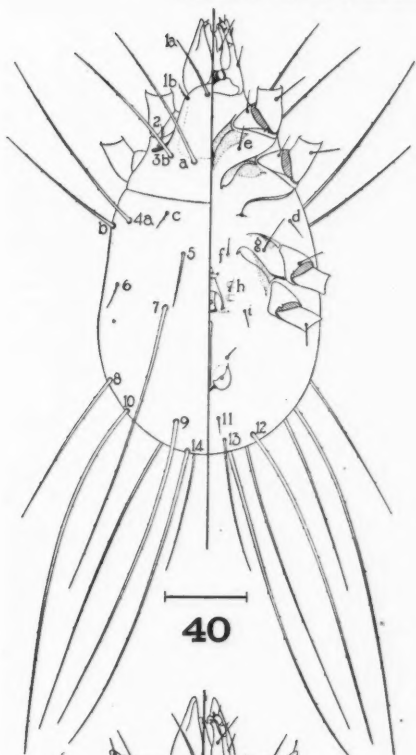


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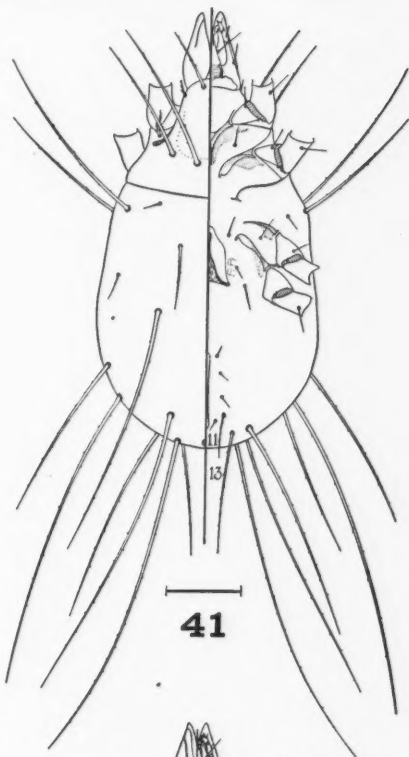


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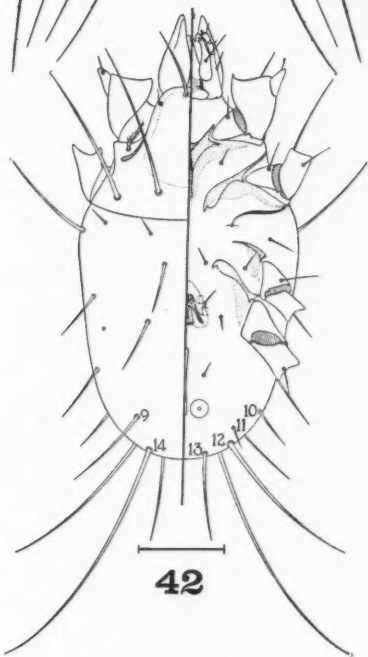




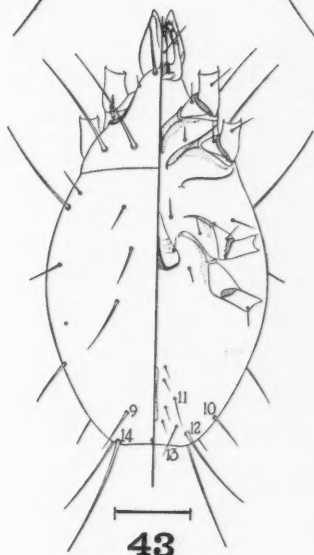
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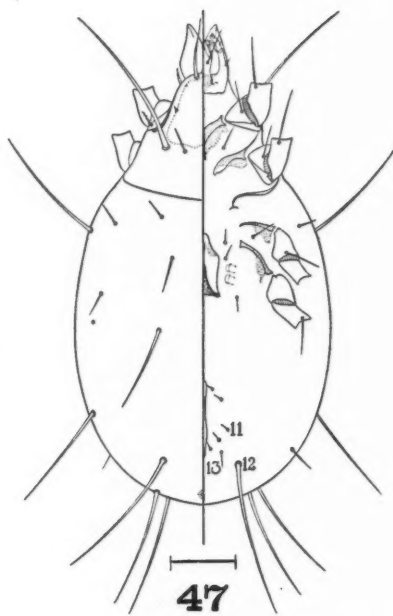
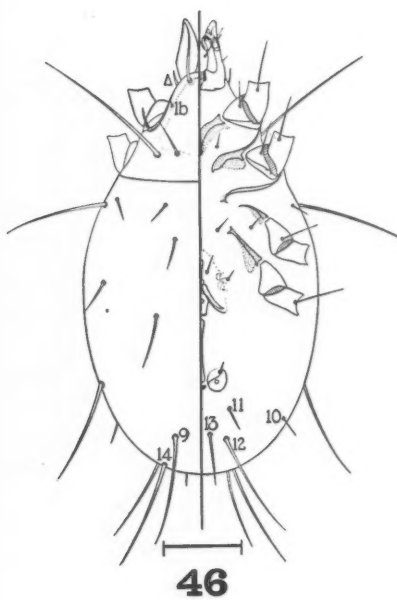
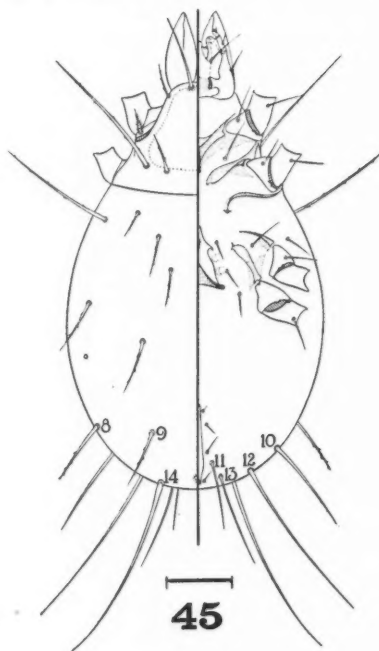
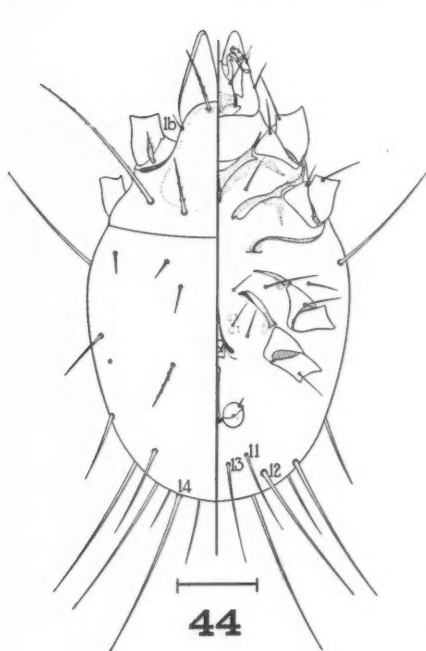
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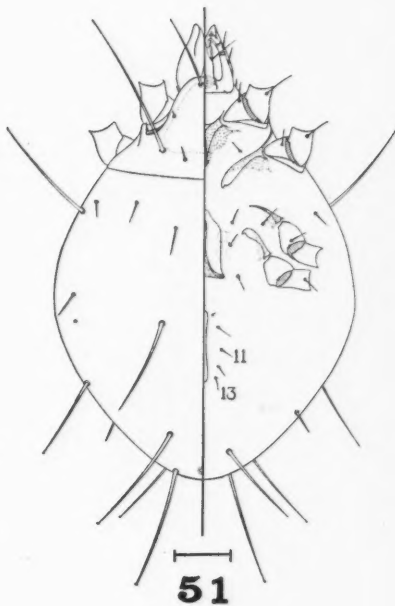
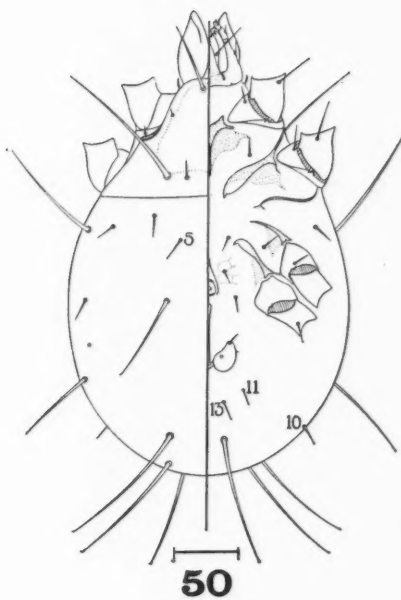
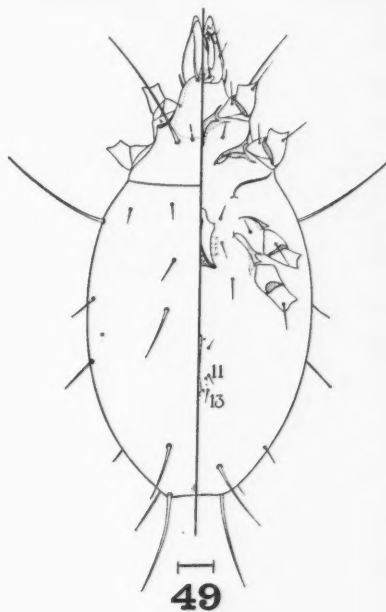
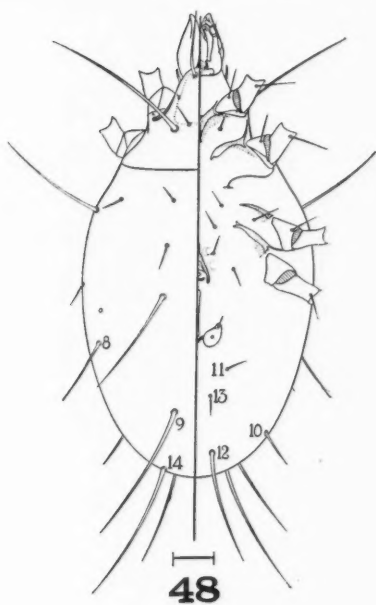


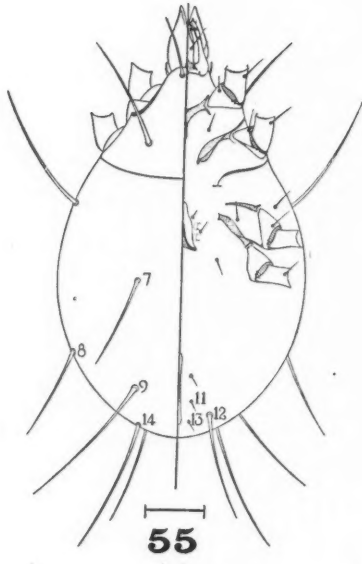
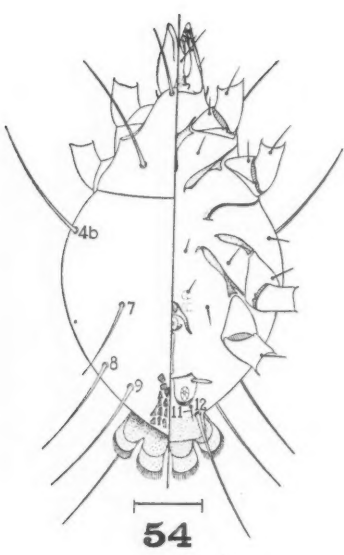
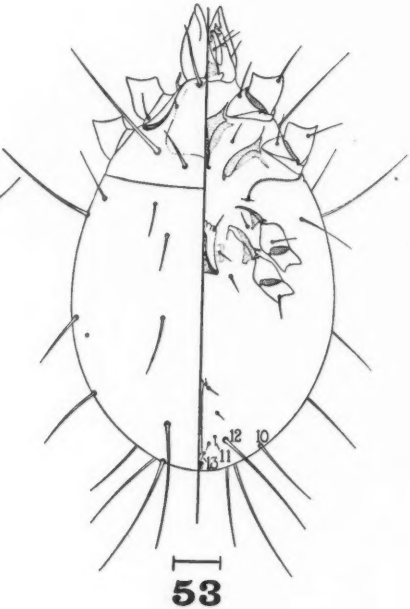
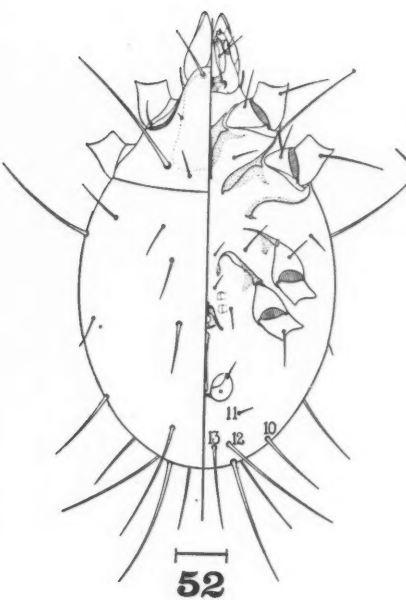
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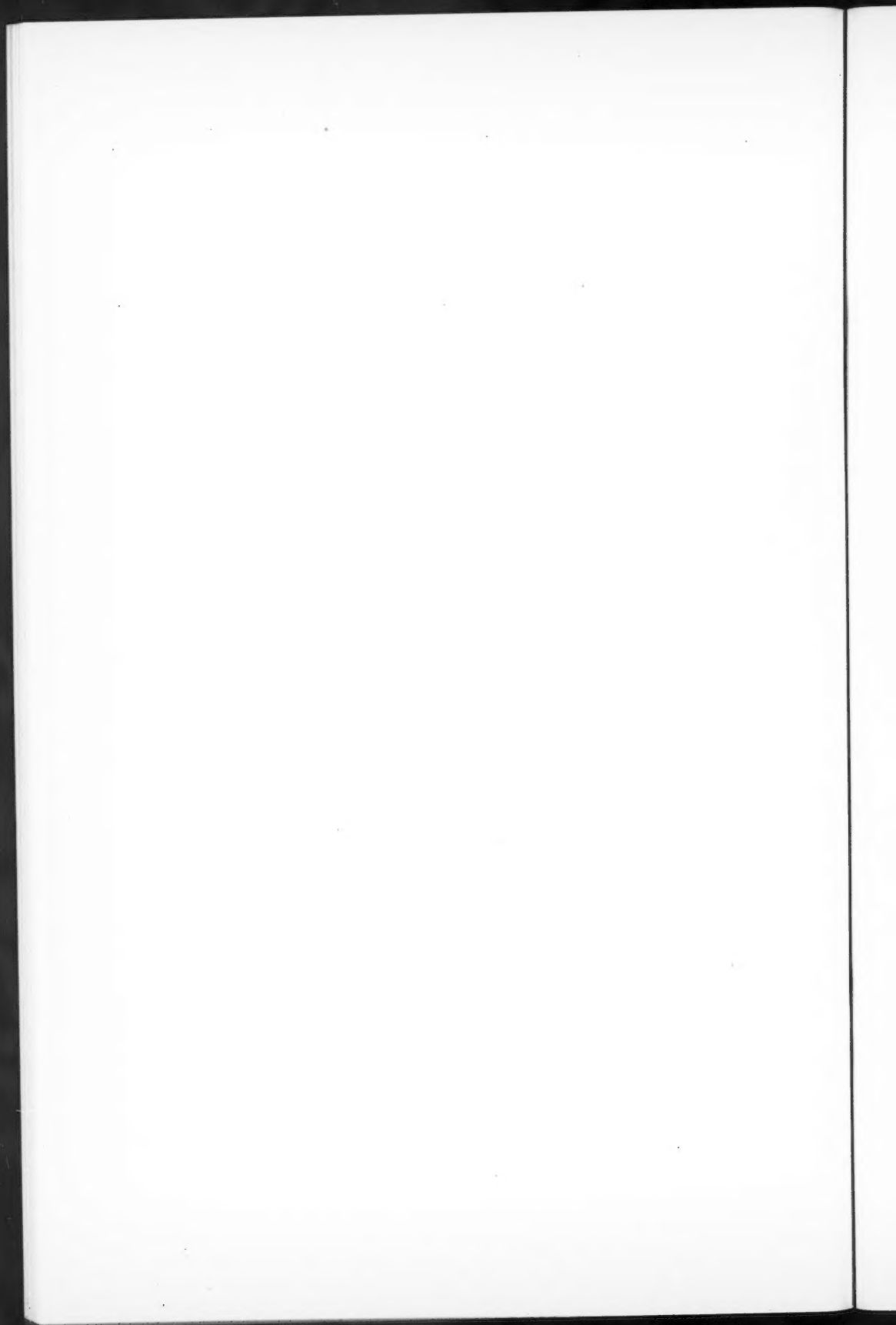
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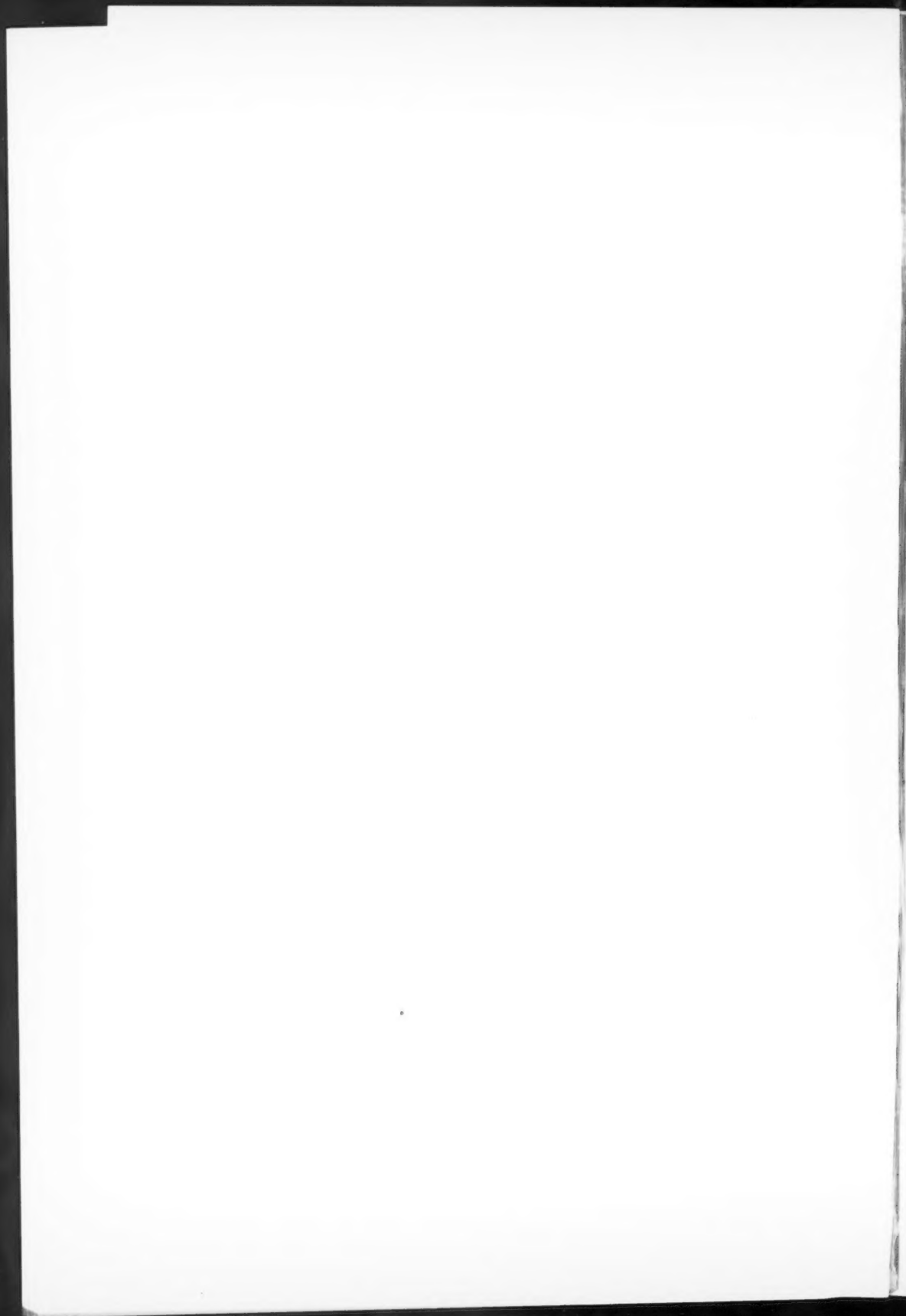
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Yolk conversion in the salmon embryo, Effect of temperature on, 7.



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